Palaeoecology of Late Ladinian (Middle Triassic) benthic faunas from the Schlern/Sciliar and Seiser Alm/Alpe di Siusi area (South Tyrol, Italy)

Friesenbichler, Evelyn ; Hautmann, Michael ; Nützel, Alexander ; Urlichs, Max ; Bucher, Hugo

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--Manuscript Draft--

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Response to Reviewers:	Ref.: Ms. No. PAZE-D-17-00052R1 Palaeoecology of Late Ladinian (Middle Triassic) benthic faunas from the Schlern/Sciliar and Seiser Alm/Alpe di Siusi area (South Tyrol, Italy)

General note: Please see attached document with “track changes” for the details of our changes in response to the reviewer’s comments.

Reviewer’s comments

AUTHOR AFFILIATIONS:
Once again, to avoid any confusion, please please split the affiliations of Alexander Nützel ... SNSB-BSPG and LMU are clearly different institutions (see my former comments)

Response: We split the affiliation of Alexander Nützel and apologize that we did not do that in the first place.

TEXT:
Page 22, line 505 ... Szulc INSTEAD OF Sculz 2007
Page 23, line 524 ... Kozur and Mostler 1973 IS MISSING in your REFERENCES
Page 23, lines 524/525 ... Mostler 1977 IS MISSING in your REFERENCES
Page 23, line 526 ... Reich 2013 IS MISSING in your REFERENCES
Page 24, line 548 ... Gaetani et al. 1981 INSTEAD OF Gaetani 1981
Page 28, line 646 ... Eichwald, E. von. 1851. INSTEAD OF Eichwald, M. 1851.
Page 28, line 646 ... Geognosie, auf INSTEAD OF Geognosie auf
Page 28, line 647 ... die Eifel, Tyrol, Italien, Sizilien INSTEAD OF die Eife, Tirol, Sizilien
Page 30, line 691 ... Gümbel, C.W. 1861. INSTEAD OF Gümbel, C.W. von 1861. ...(Gümbel was nobled in 1882)
Page 33, lines 754/55 ... implement Kozur and Mostler 1973 (see Page 23, line 524)
Page 34, lines 782/783 ... implement Mostler 1977 (see Page 23, lines 524/525)
Page 36, lines 820/821 ... implement Reich 2013 (see Page 23, line 526)
Page 36, lines 825-826 ... DELETE Sano and Nakashima 1997 which is not cited in text etc.
Page 39, line 887 ... "Trachyceras" IN ITALICS please
Page 39, line 889 ... "Myophoria kefersteini" IN ITALICS please
Page 40, line 928 ... Yin INSTEAD OF Ying
Page 41, line 930 ... Yin INSTEAD OF Ying
Page 41, line 932 ... Yin INSTEAD OF Ying
Page 43 ... line 981 ... von Eichwald, 1851 INSTEAD OF Eichwald, 1851

Response: As requested we changed the above mentioned text passages and deleted the work of Sano and Nakazawa (1997). Naturally, we added the work of Kozur and Mostler (1973), Mostler (1977) and Reich (2013) to the reference list and apologize that this mistake did not track our attention before.

REFERENCES:
Please check again my former comments (comment 5) ... Please use an en-dash NOT a hyphen netween page numbers

Response: All hyphens between page numbers were changed into en-dashes.

TABLE:
Frizzell and Exline (1956) INSTEAD OF Frizzell and Exline (1955)

Response: We changed the above mentioned text passage as requested.

ONLINE RESOURCE:
Please re-format your species names ... "sp.", "sp. 1...", "cf.", "n.sp." NOT IN ITALICS

Response: We performed the necessary changes in our electronic supplementary material.

	Further changes Independently from the reviewer's suggestions we performed some minor changes on the manuscript, which can be seen in the track-edited version of the manuscript.

Palaeoecology of Late Ladinian (Middle Triassic) benthic faunas from the Schlern/Sciliar and Seiser Alm/Alpe di Siusi area (South Tyrol, Italy)

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benefited from careful reviews by William Foster, Christopher A. McRoberts, Simon Schneider and Mike Reich.

Abstract

The Schlern and Seiser Alm area (South Tyrol, Italy) is a classical locality for studies of Middle Triassic platform to basin transitions, yet details of the palaeoecology of the rich benthic faunas of this area have been insufficiently known. We herein present a detailed palaeoecological study of the fauna from the Schlernplateau beds (late Ladinian to early Carnian) and the more or less time-equivalent Pachycardientuffe (late Ladinian), which is based on quantitative faunal data. The palaeoecology as well as sedimentary features suggest that the fauna of the Schlernplateau beds represents a lagoonal soft bottom fauna. The high species richness of the fauna as well as the locally restricted occurrences of fossils indicate an open lagoonal setting palaeogeographically close to an oceanic inlet. The high evenness of the fauna is probably a result of time-averaging. In contrast, the fauna of the Pachycardientuffe shows clear indications of transportation. Ecological features of this fauna and palaeogeographic reconstructions suggest three potential source areas: (1) the lagoon represented by the Schlernplateau beds, (2) the reef fringing this lagoon and (3) a shallow clastic coast of a nearby volcanic island and/or submarine high. A comparison between diversities of selected Early and Middle Triassic lithological units revealed the increasing species richness of all major benthic taxa during the Middle Triassic and a shift from bivalve dominated Early Triassic faunas to gastropod dominated faunas.

Keywords: Middle Triassic, biotic recovery, quantitative faunal analyses, palaeoecology, palaeoenvironment.

Kurzfassung

Obwohl das Gebiet des Schlern und der Seiser Alm (Südtirol, Italien) seit langem als klassische Lokalität für die Erforschung mitteltriassischer Plattform-Becken-Übergänge gilt, ist die Paläoökologie ihrer reichen benthischen Fauna unzureichend erforscht. Wir präsentieren eine detaillierte paläoökologische Studie der Fauna der Schlernplateau-Schichten (spätes Ladinium bis frühes Karnium) und der mehr oder weniger gleichalten Pachycardientuffe (spätes Ladinium), welche auf quantitativen Daten basiert. Die Paläoökologie sowie der sedimentologische Kontext legen nahe, dass die Fauna der Schlernplateau-Schichten eine lagunäre Weichbodenfauna repräsentiert. Ihre hohe Diversität sowie die lokal begrenzten Vorkommen der Fossilien deuten auf eine offene Lagune hin, die sich paläogeographisch nahe an einem Einlass zum offenen Meer befand. Die hohe Gleichmäßigkeit der Fauna ist höchstwahrscheinlich das Resultat von „time-averaging“. Im Gegensatz dazu gibt es in der Fauna der Pachycardientuffe klare Hinweise auf Transport. Die Ökologie dieser Fauna und paläogeographische Rekonstruktionen lassen auf drei potentielle Herkunftsgebiete schließen: (1) die Lagune, welche durch die Schlernplateau-Schichten repräsentiert wird, (2) das Saumriff dieser Lagune und (3) eine flache, siliziklastische Küste nahe einer vulkanischen Insel und/oder einer submarinen Hochzone. Ein Vergleich der Diversitäten ausgewählter früh- und mitteltriassischer lithologischer Einheiten offenbart einen Anstieg der Diversität während der Früh- und Mitteltrias sowie einen Wechsel von Muschel-dominierten frühtriassischen Faunen zu Gastropoden-dominierten Faunen während der Mitteltrias.

Schlüsselwörter: Mitteltrias, ökologische Erholung, quantitative Faunen-Analysen, Paläoökologie, Paläo-Umwelt.

1. Introduction

The recovery from the end-Permian mass extinction, which killed between 81% (Stanley 2016) and 96% (Raup 1979) of marine species, provides a unique test-case for studying long-term evolutionary responses to a sudden and massive loss of species on a global scale. Scientific interest in studying the recovery pattern is twofold: it allows testing macroevolutionary models (e.g., Brayard et al. 2009; Hautmann et al. 2015), and it represents a (pessimistic) analogue for the long-term future of biosphere in the face of anthropogenically caused environmental changes (Payne and Clapham 2012).

Understanding evolutionary processes requires the study of species in their ecological context. Concerning the recovery from the end-Permian mass extinction, much palaeoecological work has been done in the past decades, but these studies almost exclusively concentrated on the Early Triassic (e.g., Schubert and Bottjer 1995; Twitchett and Wignall 1996; Hofmann et al. 2013a, 2013b, 2014, 2015; Hautmann et al. 2011, 2015; Foster et al. 2017), which is the ca. 4 Ma time interval that followed the end-Permian mass extinction. However, biodiversity in terms of global taxonomic richness did not reach the pre-extinction level before the Late Jurassic (Sepkoski 1997) or later (Alroy et al. 2008). With regard to alpha-diversity in local environments, the major recovery step seems to have taken place during the Middle Triassic, as evidenced by the striking differences between most diverse Early Triassic communities that include around 45 benthic species (Hautmann et al. 2013, 2015; Hofmann et al. 2013b, 2014) and, e.g., the hyperdiversified fauna from the Longobardian–Julian (Late Ladinian–Early Carnian) Cassian Fm. of northern Italy (>1000 benthic species; Tab. 1). The progress in recovery during the Middle Triassic has been addressed in several recent studies (e.g., Payne 2005; Payne et al. 2006; Song et al. 2011; Velledits et al. 2011; Foster and Sebe 2017) but data are still relatively scarce.

This study is based on quantitative bed-rock sampling in the area of Schlern/Sciliar mountain and Seiser Alm/Alpe di Siusi (South Tyrol, Italy; Fig. 1), which is a paradigm for a Middle to Late Triassic reef-to-basin landscape. It is one of the few places in the world where the platform-slope-basin transitional zone is preserved in its primary setting (Keim 2008; Brandner et al. 2016), giving the

opportunity to study the ecology of concurrent faunas in different environments. Sampling was carried out (1) in sediments of a lagoonal setting represented by the locally highly fossiliferous Schlernplateau beds on the Schlern mountain and (2) in the basinal setting of the 'Pachycardientuffe' at the Seiser Alm, which represent approximately the same stratigraphic age (see chapter 3). The palaeoecology and species distributions of both faunas are discussed in the context of their depositional environments, and their diversities are compared with published data on Early–Middle Triassic benthic communities from other regions, which allows preliminary insights into diversity changes through the Early and Middle Triassic time interval.

2. Material and Methods

Fieldwork was carried out in August 2016 at the Seiser Alm/Alpe di Siusi and the Schlern/Sciliar mountain in South Tyrol/Alto Adige in northern Italy. At the Seiser Alm, fossils were sampled in the gorge of the Frommerbach/Rio Frommer and one of its eastern tributaries (Figs 1 and 2a-b). On the Schlern, fossils were mainly collected on the western flank of the Seiser Klamm/Gola di Siusi (Figs 1 and 2c-d). Outcropping rock material of fossiliferous beds was quantitatively sampled until the occurrences of fossils were exhausted. Additionally, fossils quantitatively collected by M. Urlichs between 1998 and 2012 at the same localities were included in the analyses. Specimens used for the palaeoecological analyses are housed at the State Museum of Natural History Stuttgart (Germany, inventory numbers SMNHS17501/250 - SMNHS75538) and the Museum of Nature South Tyrol (Italy, inventory numbers PZO5980 - PZO5998). For taxonomic identification fossils were first washed and then, when necessary, prepared with micro jacks. A quantitative matrix of fossil occurrences was compiled at species level (Online Resource 1). For bivalves, the number of individuals has been inferred by counting only the most numerous valves (left or right) together with articulated specimens. Only fossils that (1) were clearly relatable to specific beds of the investigated outcrops

and (2) samples with more than 40 individuals were used for palaeoecological data analyses. Sedimentological observations in the field and information from ecological analyses were used for the interpretation of the depositional environment. Our complete dataset comprises 2723 individuals assigned to 53 species for the Schlernplateau beds and 651 individuals assigned to 59 species for the Pachycardientuffe.

Ecological parameters and statistical analyses were calculated using the software PAST, version 2.17 (Hammer et al. 2001). Based on the species-abundance data, rarefaction analyses were carried out for each sample in order to compare species richness of faunas with different sample sizes and to assess the relative completeness of sampling. For further ecological characterization, rank-abundance distributions, trophic nuclei, and ecological pie charts were used. The trophic nucleus of an association comprises those species that contribute 80% of the total number of individuals in an association (Neyman 1967). Following Aberhan (1994), species were assigned to 10 trophic guilds, based on functional morphology, mode of life of related Recent species, information from the literature, and the sedimentological context. Gastropods were collectively assigned to epifaunal herbivores and/or detritus-feeders, since evidence for more specialized feeding lacks. For the identification of recurrent assemblages and groups of ecologically related species, Q-mode cluster analyses were calculated for samples containing more than 40 individuals, using the Morisita similarity index (Morisita 1959) and unweighted pair-group average. Additionally, R-mode cluster analyses were used for the identification of sets of species that typically co-occur.

3. Geologic setting

The Schlern and the adjacent Rosengarten/Catinaccio represent a Middle Triassic carbonate platform with northeastward, eastward to southeastward inclined reef slopes (Brandner 1991;

Bosellini 1998; Brandner et al. 2007; Keim 2008). Towards the west, there was probably a connection to the Mendel platform (Keim 2008). The Schlern Mountain is build up by (1) the pre-volcanic, up to 800 m thick 'Schlerndolomite' (Rosengarten Fm.), (2) up to 40 m thick volcanic rocks and (3) post-volcanic, well-bedded dolomite formerly known as 'Rosetta Dolomite' or 'Cassian Dolomite', now interpreted as the platform facies of the Rosszähne Fm. The latter is overlain by (4) the Schlernplateau beds, which is a sequence of carbonate rocks and grey to reddish marls that are locally highly fossiliferous and commonly interpreted as lagoonal sediments (Figs 2c-d; Keim 2008; Brandner et al. 2016). Findings of the biostratigraphically important ammonoid *Prototrachyceras archelaus* (Laube, 1869b) indicate a Late Ladinian age of the Schlernplateau beds (Brandner 1991; Urlichs and Tichy 2000). However, the occurrence of the bivalve *Myophoria kefersteini kefersteini* (Münster in Goldfuss, 1837) in the uppermost 6 m of the Schlernplateau beds suggests that the top of the formation extends into the Lower Carnian (Urlichs 2014). The thickness of the Schlernplateau beds varies from only a few meters to a maximum of ca. 40 m. Towards the platform margins, the Schlernplateau beds interfinger with the reef flat facies.

During deposition of the Rosszähne Fm. and Schlernplateau beds at the top of the Schlern carbonate platform, the adjacent Seiser Alm basin was filled with a more than 500 m thick successions of volcanoclastic detritus of the Wengen Fm. and, later, the mixed siliciclastic-carbonate succession of the St. Cassian/San Cassiano Fm. (Brandner 1991). Within the Wengen Fm. of the Seiser Alm, the Late Ladinian (Urlichs 1977, 1994, 2014) 'Pachycardientuffe', which are named for the mass occurrence of the bivalve *Pachycardia rugosa* von Hauer, 1857, represent several (at least two) conglomeratic, highly fossiliferous intercalations that have been mapped as distal parts of the 'Marmolada Conglomerate' in the geological map of the western Dolomites (Autonome Provinz Bozen (ed.) 2007). However, the Marmolada Conglomerate in the strict sense is a volcanogenic conglomerate that was transported from a source area near the Marmolada Mountain (ca. 20 km east of the study area) into adjacent basins (e.g., Bosellini 1998; Bottoli and Trombetta 1998). In contrast, the lithology of the Pachycardientuffe is dominated by non-dolomitized limestone pebbles

and cobbles (small to medium sized 'Cipit boulders') that originate from adjacent carbonate platforms. We therefore assume that the Pachycardientuffe represent distal equivalents of tongues of foreslope talus deposits, as described by Yose (1991) in a proximal facies at the Mahlknecht cliff, around 4 km SE of our sampling localities. The admixed volcanogenic pebbles and volcanoclastic matrix could either have been taken up during transportation, or stem from a second source area, or could represent the result of mixing of carbonate and volcanogenic components by reworking (see chapter 5.2.).

4. The Schlernplateau beds

Early workers erroneously correlated the fauna of the Schlernplateau beds with the younger Raibl Fm. (Carnian), based among other reasons on the occurrence of *Myophoria kefersteini* (Münster in Goldfuss, 1837; e.g., von Richthofen 1860). This view was also shared by von Wöhrmann and Koken (1892) in their comprehensive description of the Schlernplateau fauna and was maintained by most subsequent authors until Brandner (1991), Urlichs and Tichy (2000) and Urlichs (2014) provided evidence for a Late Ladinian (*Prototrachyceras archelarus–Frankites regoledanus* ammonoid zone) to early Carnian (*Daxatina canadensis* ammonoid zone) age. In addition to ammonoid finds, the key observation for the revised stratigraphy was the existence of several subspecies of *Myophoria kefersteini*, which are indicative of different stratigraphic intervals (Urlichs 2014). With this updated stratigraphic information, Schlernplateau beds and Pachycardientuffe are more or less time-equivalent units.

Von Wöhrmann and Koken (1892) described 72 species, including 33 gastropod species, 24 bivalve species, eight cephalopod species, three echinoid species, two coral species and one crinoid species from the Schlernplateau beds. Notably, nearly all specimens of this rich fauna stem from a

limited area at the western flank and southern part of the Seiser Klamm. The only other locality that is explicitly mentioned in von Wöhrmann and Koken (1892) is the 'Burgstall', some hundred meters east of the Seiser Klamm, where one coral species (*Thecosmilia rothpletzi* von Wöhrmann and Koken, 1892), fragments of crinoids and echinoid spines were found. Our survey confirms that fossils are scarce or absent at other places of the Schlernplateau. At the Seiser Klamm locality, fossils are most abundant in the upper part of the section, particularly in several layers of red marl (Fig. 3). Fossils are also abundant in several rudstone beds near the top of the section (Fig. 2e), but the crystallized limestone makes it difficult to extract them from the matrix.

A detailed section was measured at the western flank of the Seiser Klamm and samples were taken from three localities on the Maultierrücken/Dorsale del Mul (Figs 1 and 3). The investigated section starts with an alternation (ca. 20 m) of partly dolomitic limestone beds, which are separated by marls or covered intervals that probably also represent fine-grained sediments. The limestone and dolomite beds are mud-, wacke-, pack- and grainstones that sometimes contain bioclasts like bivalve and gastropod shells and, less common, ooids. The overlaying marl beds (SP3 and SP5) are highly fossiliferous. Above these marls, an around 3 m thick sequence of thick-bedded wackestone forms a prominent cliff, the top of which is formed by a 30 cm thick oolitic limestone bed (at a height of 25 m). Several marly, highly fossiliferous intervals above this cliff provided the majority of fossils studied herein. Within the marly intervals, laterally discontinuous oolithic limestone beds are repeatedly intercalated, which sometimes contain bioclasts such as gastropod and bivalve shells. A notable lithological marker bed near the top of the section contains shell debris, ooids, and interspersed pisolithic iron ore grains. Surface ornamentations on the fossils are generally well preserved. This lack of abrasion as well as the fact that some bivalves were preserved with conjoined valves indicate that the fossils were not transported over larger distances. According to Urlichs and Tichy (2000) and Urlichs (2014) the uppermost layers of the investigated section are already Carnian in age. Accordingly, the Ladinian/Carnian boundary lies within fossiliferous bed SP10 (Fig. 3).

4.1. Fauna of the Schlernplateau beds

A total number of 53 species occurring in 16 fossiliferous beds (SP1-SP16, Fig. 3) was identified, including 27 gastropod species, 19 bivalve species, four coral species and one sponge species (Online Resource 1). Notably, brachiopods are absent, and only one crinoid columnal fragment and one echinoid spine were found. In terms of species richness, our collection is comparable to the diversity described in the monograph of von Wöhrmann and Koken (1892; 72 species). Species richness within the different beds varies between 2 to 32. However, rarefaction analyses of samples from each fossil horizon indicate different degrees of sampling completeness (Fig. 4a).

The 10 most frequent species are, in descending order, *Myophoria kefersteini* (Münster in Goldfuss, 1837) (bivalve, 16.3%), *Heminajas fissidentata* (von Wöhrmann, 1889) (bivalve, 11.4%), *Pachycardia rugosa* von Hauer, 1857 (bivalve, 9.7%), *Neritaria plicatilis* (von Klipstein, 1844) (gastropod, 8.3%), *Naticopsis neritacea* (Münster, 1841) (gastropod, 8%), *Coelostylina solida* (von Wöhrmann and Koken, 1892) (gastropod, 5.8%), *Palaeonarica concentrica* (Münster, 1841) (gastropod, 4.3%), *Myophoriopis richthofeni* (Stur, 1868) (bivalve, 4%), *Trigonodus rablensis* (Gredler, 1862) (bivalve, 3.8%) and '*Loxonema*' *aequale* von Wöhrmann and Koken, 1892 (gastropod, 3.3%). These 10 species together with *Cassianella bipartita* (von Klipstein, 1845) (bivalve, 3.2%) and *Stephanocosmia coronata* (von Wöhrmann and Koken, 1892) (gastropod, 3%; Fig. 5 and 6) constitute the trophic nucleus of the complete fauna at the Schlernplateau. Simpson's index of dominance of associations from different fossiliferous beds is generally high and varies between 0.06 and 0.30, with an average value of 0.2 (Online Resource 1).

Cluster analysis (Fig. 7) did not reveal the existence of clearly distinct associations. However, a cluster of samples that are dominated by *Myophoria kefersteini* is set off from samples in which species of *Pachycardia* and *Trigonodus* are more abundant. Because *Myophoria*, *Trigonodus* and *Pachycardia* are not only phylogenetically closely related but also ecologically similar (both are

shallow infaunal suspension feeders), we do not believe that these two clusters represent fundamentally different environmental conditions. As an alternative explanation, it seems possible that haphazardness of larvae settlement had randomly favoured different dominant species at different times.

Although the fauna of the Schlernplateau beds is gastropod dominated in terms of species richness, it is bivalve dominated in terms of total number of individuals. Accordingly, most species were epifaunal herbivores and/or detritus-feeders, whereas almost half of all collected individuals are shallow infaunal suspension-feeders, followed by epifaunal herbivores and/or detritus-feeders and free-lying epifaunal suspension-feeders (Fig. 8a). However, the guild-specific diversity and absolute abundance of trophic guilds can vary between different fossiliferous beds (Fig. 9).

Frequency distributions of assemblages from different fossiliferous beds show different patterns, but a remarkable aspect is that many show an unusually high degree of evenness (Figs 9b-c). The lack of abrasion, occurrence of bivalves with conjoined valves, and the sedimentological context (occurrence in fine-grained sediments) exclude that this pattern is due to effects of faunal mixing by transportation. Another notable aspect is that there are often lateral differences in the faunal composition within single fossiliferous beds (Fig. 9).

4.2. Interpretation of the Schlernplateau fauna

The geologic context leaves little doubt that the Schlernplateau beds represent lagoonal sediments of the platform interior. This is evident by the sedimentary features of the Schlernplateau beds themselves, which include the coexistence of high- and low-energy sediments (e.g., oolites and shell coquinas (rudstones) versus marls, wackestones, and early diagenetic dolomites) and the presence of locally abundant oncoids (Fig. 2f). It is further corroborated by the lateral facies change, which includes the transition to fringing coral reefs on the supposed seaward side and to pedogenic

sediments at places where the platform was emerged (Brandner et al. 2016 and own observations). Finally, the ecology of the documented fauna is in accordance with a lagoonal setting because shallow infaunal suspension-feeders and free-lying epifaunal suspension-feeders dominate, which are commonly associated with a soft substratum.

Given the lagoonal setting, two aspects of the Schlernplateau fauna are remarkable. First, the species richness is unusually high for this environment. Although decidedly stenohaline organisms lack (e.g., brachiopods) or are extremely rare (e.g., echinoderms and ammonoids), the high species richness excludes that the lagoon was (at the place where the samples were taken) affected by high environmental stress such as changing salinity, which often characterizes restricted lagoons (e.g., Fürsich 1994; Fürsich et al. 1995). The second unusual aspect is the extremely high evenness in many samples. Based on the state of preservation and the occurrence in marly beds (see above), faunal mixing by transportation can be excluded. However, no examples of primary causes for such high evenness are known to us from ecologically comparable faunas. We therefore assume that the high evenness may, at least partly, reflect the effects of time-averaging. Fürsich and Aberhan (1990) nicely demonstrated how time-averaging may produce abundance patterns similar to those that we observed in the Schlernplateau beds.

Our summary interpretation of the sedimentological and faunistic data is that the Schlernplateau beds represent an open lagoon and that the outcrop area around the Seiser Klamm was palaeogeographically close to an oceanic inlet that prevented large-scale fluctuations in salinity and temperature, provided supply of food for filter feeding organisms, and was the source of larvae that settled within the lagoon. The randomness in the composition of larvae that reached the lagoon may be partly responsible for differences in the faunal composition. In this model, successive communities went back to different settlement events, each with a particular taxonomic composition of larvae and thus resulting in different dominance of the resulting cohort. Superimposition of abundance patterns of successive communities by time-averaging then caused a pattern where many species are nearly equally abundant. However, prevalent species probably dominated at different

times. We note that time-averaging might have also contributed to the high overall species richness, but even if this effect is considered, the Schlernplateau beds are still remarkably species rich.

Additional support for the open lagoon model comes from the fact that fossil occurrences are locally restricted (close to oceanic inlets in our interpretation). From a sedimentological perspective, the laterally discontinuous oolitic limestone beds that are intercalated in the low-energy marls probably represent washover deposits from a nearby barrier, which however was discontinuous near the fossil locality.

5. The Pachycardientuffe/Tufi a Pachycardie

Like the fauna from the Schlernplateau beds, the highly diverse fauna of the Pachycardientuffe is known for more than 100 years. Broili (1903) described 157 species, including 122 bivalve species, 18 brachiopod species, 13 echinoid species and four crinoid species. Blaschke (1905) added the description of 77 gastropod species, as well as three sponge species, five coral species, one scaphopod species and 14 bivalve species that were not described in Broili (1903). A detailed description of brachiopods from the Pachycardientuffe was given by Waagen (1903). After a revision by Waagen (1907) a total number of 165 bivalve species is described from the Pachycardientuffe. Overall, more than 270 species have been reported from the Pachycardientuffe thus far (Tab. 1). It should be noted, however, that some of the major fossil localities (e.g., at the Tschapitbach/Rio Cipit) are currently covered and therefore not accessible.

The investigated section at locality Frommerbach A is located in the gorge of the Frommerbach itself (Figs 1, 2a and 10). It starts with a fossiliferous conglomerate at 1850 m altitude that overlies volcanoclastic sandstone beds of the Wengen Fm. with an erosional disconformity. The pebbles are mainly limestones and less commonly rounded volcanic rocks, which are embedded in a siltstone

matrix. The overlaying bedded sandstone contains limestone blocks at its top. The components of the following fossiliferous conglomerate consist of limestone and volcanoclastics. After a 3 m thick interval of siltstone, highly fossiliferous sandy siltstones follow on top of this section. The investigated section Frommerbach B is located in an eastern tributary of the Frommerbach (Figs 1, 2b and 10) at 1850 m altitude. The rocks are matrix supported, fossiliferous, pebble bearing, volcanogenic, middle- to coarse grained sandstones. As pointed out by Urlichs (2014), the fossiliferous rocks in the two Frommerbach sections do not belong to the same horizon. The investigated rocks of section Frommerbach A are younger than the rocks from Frommerbach B. For a detailed stratigraphic correlation between the sections see Fig. 3 in Urlichs (2014).

5.1. Fauna of the Pachycardientuffe

At the two Frommerbach localities a total number of 59 species was found, which is much less than the overall species richness of the Pachycardientuffe (277 species), as described in Broili (1903), Waagen (1903), Blaschke (1905) and Waagen (1907). These 59 species include 30 bivalve species, 16 gastropod species, five echinoid species, three coral species, three crinoid species and two brachiopod species. Sponges are absent. The seven most frequent species are, in descending order, *Pachycardia rugosa* von Hauer, 1857 (54.4%), *Pachycardia plieningeri* Broili, 1903 (27.3%), *Trigonodus rablensis* (Gredler, 1862) (3.7%), *Myophoria kefersteini* (Münster in Goldfuss, 1837) (1.8%), *Fedaiella inaequiplicata* (von Klipstein, 1843) (gastropod, 1.4%), *Naticopsis seisiensis* (Blaschke, 1905) (gastropod 1.2%) and *Heminajas fissidentata* (von Wöhrmann, 1889) (1.1%; Figs 5 and 6). The fauna is clearly dominated by the two bivalve species *Pachycardia rugosa* and *Pachycardia plieningeri* that form the trophic nucleus. All other species are relatively rare and almost half of the species is only represented by one individual (Figs 8b and 11). Simpson-D ranges between

0.29 and 0.47, with an average value of 0.39 (Online Resource 1). Again, the rarefaction analysis shows that the diversity of some samples is underestimated (Fig. 4b).

A palaeontological analysis of the fauna from the Pachycardientuffe was already performed by Fürsich and Wendt (1977), based on 283 individuals belonging to 26 species, including bivalves (11 species), gastropods (11 species), crinoids (two species), echinoids and corals (one species, respectively). This analysis shows a similar rank-abundance pattern as in our study. *Pachycardia rugosa* is with 85.5% the most abundant species, whereas almost three-quarters of all species are represented by only one individual. Because Fürsich and Wendt (1977) did not separate *Pachycardia rugosa* and *Pachycardia plieningeri*, the Simpson-D in their study is relatively higher (0.71) than in our study (min. D = 0.29; max. D = 0.46). Whether *P. rugosa* and *P. plieningeri* represent two different species is debatable. In this study, we used the less deeply depressed lunule and the more posterior position of the beaks in *P. plieningeri* as criteria for their separation. Additional criteria noted by Broili (1903) include a more elongated outline and more elongated, but narrower anterior cardinal tooth in *P. plieningeri*.

The fauna of the Pachycardientuffe is bivalve dominated in terms of species richness and total number of individuals. The guild-species diversity shows that epifaunal herbivores and/or detritus-feeders, epibyssate suspension-feeders and shallow infaunal suspension-feeders are the most important guilds (Fig. 8b). However, most individuals belong to shallow to moderate deep infaunal suspension-feeders, which is not surprising since both dominating species belong to this group.

5.2. Interpretation of the fauna from the Pachycardientuffe

Several lines of evidence indicate that the fauna of the Pachycardientuffe is allochthonous: (1) the lack of fossils that were preserved in life position; (2) the lack of bivalves that are preserved with

conjoined valves; (3) frequent fragmentation of fossils; (4) the poorly sorted sediment. These observations raise the question where the transported fossils originally came from.

In contrast to the Schlernplateau fauna, where many species occur in similar abundances, the fauna from the Pachycardientuffe is clearly dominated by only two species, namely *Pachycardia rugosa* and *Pachycardia plieningeri*. A comparison between the fauna of the Schlernplateau beds and the Pachycardientuffe revealed that 45% of all species occur exclusively in the Pachycardientuffe and 38% of all species occur exclusively in the Schlernplateau beds. The remaining 17% of all species occur in the Schlernplateau beds as well as in the Pachycardientuffe (Online Resource 1). Species that occur in the Schlernplateau beds as well as in the Pachycardientuffe include the bivalve species *Myophoria kefersteini*, *Heminajas fissidentata*, *Pachycardia rugosa*, *Myophoriopis richthofeni* and *Trigonodus rablensis*, which belong to the most abundant species in the Schlernplateau beds as well as in the Pachycardientuffe. All these species were shallow infaunal suspension-feeders that required a soft substratum. However, there are large differences in the relative abundances of these species between the Schlernplateau beds and the Pachycardientuffe. *Myophoria kefersteini* and *Heminajas fissidentata* are the most common species in the Schlernplateau beds but only occur rarely in the Pachycardientuffe. In contrast, *Pachycardia rugosa* is the dominant species in the Pachycardientuffe, but it ranks third in the Schlernplateau beds, where it is much less common than *Myophoria kefersteini* and *Heminajas fissidentata*. If the Schlernplateau beds were the only source area for the fossils of the Pachycardientuffe, then *Pachycardia rugosa* should be less dominant. It is therefore likely that the fauna of the Pachycardientuffe did not originate solely from the Schlernplateau beds.

Based on palaeogeographic reconstructions (Brandner 1991, p. 12, Fig. 6; own observations) and ecological features of the fauna, we identified two additional possible source areas for the fauna of the Pachycardientuffe. One of these additional source areas is the shallow clastic coast of a nearby volcanic island and/or adjacent submarine highs, where a fauna could have flourished in volcanoclastic sediments. Brandner (1991, p. 12, Fig. 6) indicated the presence of a structural high with a volcanic island topography few kilometres southeast of the Frommerbach localities, which was

caused by the tectonic activity during the Late Ladinian and consisted of uplifted volcanoclastics of the Wengen Fm. Thick shelled, shallow-burrowing bivalves such as *Pachycardia* are typical faunal elements of such shallow-marine, sandy sediments (Stanley 1970). Brandner (1991, p. 12, Fig. 6) indicated dipping of the palaeo-relief of the structural high towards the northwest, directly pointing towards the Frommerbach localities (see also Yose 1991, p. 35). We assume that at least parts of the fauna of the Pachycardientuffe were transported from this source area via submarine high-density gravity flows, together with volcanogenic material (Figs 12a-c). A similar scenario was already described by Fürsich and Wendt (1977), who assumed that the high number of *Pachycardia* indicates a distinct association in a shallow-water high-energy environment, e.g. in the vicinity of volcanic swells or islands, and that this *Pachycardia* dominated fauna together with tuffitic material and faunal elements from neighbouring biotopes was transported into the basin.

A third possible source area is the reef environment that fringed the lagoon of the Schlernplateau beds. Blaschke (1905, p. 219) reported the presence of several bivalve taxa in the Pachycardientuffe that have previously been reported from the reefal facies of the "Schlerndolomit" *sensu lato*. These bivalves include *Chlamys* (*Granulochlamys*) cf. *tubulifera* (Münster, 1841), *Mysidioptera* cf. *aviculaeformis* Broili, 1903, *Mysidioptera* cf. *incurvostriata* (Gümbel, 1861), *Mysidioptera* cf. *spinigera* Bittner, 1895, *Mysidioptera acuta* Broili, 1903, *Mysidioptera* cf. *laczkói* Bittner, 1901, *Cassianella decussata* (Münster, 1841), *Waagenoperna* cf. *planata* (Broili, 1903), *Pteria* aff. *seisiana* (Broili, 1903) and *Badiotella* sp., which were mostly epibyssate suspension-feeders that needed a hard substratum for attachment. Furthermore, gastropods from the family Patellidae were reported from the Pachycardientuffe (Blaschke 1905), which also live on hard substratum.

Fig. 13 provides a summary of our interpretation of the fauna from the Pachycardientuffe, showing transportation from the following three sources: (1) the soft ground lagoonal fauna of the Schlernplateu beds, (2) the hard ground reef fauna from the Schlerndolomite and (3) a *Pachycardia rugosa* dominated fauna from the coast from a near volcanic island.

As mentioned above, the number of species found in this study (59 species) is much lower than the number of species described by Broili (1903), Blaschke (1905), Waagen (1903) and Waagen (1907; altogether more than 270 species). One explanation for the high number of species described in these monographs is taxonomic oversplitting. A taxonomic revision of the fauna is beyond the scope of this study, but an inspection of Broili's (1903) type material in Munich confirms that his taxonomic approach was more typological than usually applied today, and that e.g. the species richness of the limid bivalve genus *Mysidioptera* (24 reported species) has been clearly overestimated. However, also the number of reported genera is higher in the literature than in our samples (100 versus 38 genera), thus oversplitting of species is not the sole reason for the difference in reported diversity. An additional factor that contributed to the higher species richness in the historical monographs is probably that these were based on a higher number of geographically distant sampling localities, which likely had different source areas and thus differed considerably in their taxonomic composition. Therefore, the lower species richness in our samples might by largely due to the poorer present-day outcrop conditions, which limited our field collections to two nearby localities.

6. Summarized interpretation of the benthic faunas from the Schlernplateau beds and Pachycardientuffe

Our field study led to the recognition of 52 species in the Schlernplateau beds and 59 species in the Pachycardientuffe. The sedimentological and palaeontological analyses outlined above allow the detailed palaeoecological interpretation of these faunas.

The recorded species from the Schlernplateau beds lived in a lagoon, close to an oceanic inlet. The fauna is unaffected from mixing by transportation, but it was probably subject to some time-

averaging. This means that some of the recorded species did not live contemporaneously at the same place, thus the overall number of species is a certain overestimation of the community species richness at a given time. However, the overall diversity of the Schlernplateau fauna represents a good estimation of the taxonomic richness of shelly soft-bottom dwellers in a shallow-water setting of a tropical sea at the end of the Middle Triassic.

In contrast to the Schlernplateau beds, the fauna of the Pachycardientuffe represents almost certainly palaeocommunities from at least three different settings (lagoon, reef and sandy shallow sea) that were mixed during transportation into the basin. The fact that our collection contains significantly less species (59) than recorded in the literature (>270) is largely due to the lower number of sampled localities that encompass a lower number of ecologically different source areas.

The evidence for faunal mixing in the Pachycardientuffe does not invalidate the data for studies of biodiversity during the Middle Triassic, but it poses some constraints on their interpretation. The fauna of the Pachycardientuffe does not represent a single palaeocommunity, but an integral of the shallow marine shelly fauna that lived in different habitats at the same time. It is thus a good estimator for the gamma-diversity of the reef-to-basin landscape of the tropical Tethyan ocean during the late Middle Triassic.

7. Species richness of Early and Middle Triassic benthic faunas: a comparison

To what extend do Early and Middle Triassic benthic communities differ in their ecology, species richness and taxonomic composition? Answering this question is crucial for identifying evolutionary processes during the main phase of rediversification after the end-Permian mass extinction. We here present a preliminary comparison between selected benthic communities of these two epochs. Data used for this comparison are shown in Tab. 1. Lower and Middle Triassic macroinvertebrate faunas

selected for the comparison come from lithological units that represent similar shallow-marine environments. Because most of the data used for this comparison are raw data from the literature, synonyms and taxonomic oversplitting (see also chapter 5.2) may cause a certain bias towards greater richness, especially in Middle Triassic faunas where modern revisions mostly lack. A reevaluation of bivalve species from the Jena Fm. and the Meissner Fm. (Hautmann, unpublished data) suggests oversplitting by nearly 50%. However, because oversplitting is likely similar in all major taxa, the gastropod/bivalve ratio discussed below is probably robust, and a pronounced Anisian rise in diversity maintains even if an overestimation of diversity by factor 2 is assumed.

The comparison between Early and Middle Triassic benthic communities shows clearly that the overall diversity increased through time; however, diversity slowly increased during the Early Triassic and rapidly during the Middle Triassic (Tab. 1; Fig. 14a). This pattern is evident in the trends of the most diverse taxa in Early and Middle Triassic benthic communities, i.e., bivalves, gastropods and brachiopods. Our compilation shows that bivalves were clearly the most diverse taxon in Early Triassic benthic communities. Although bivalves were relatively diverse immediately after the end-Permian mass extinction, the net increase in species richness was small until the end of the Early Triassic. The major diversification of bivalves occurred during the Anisian (Hautmann 2007; Tu et al. 2016). Already the Late Bithynian–Early Illyrian Jena Fm. yields a highly diverse Middle Triassic bivalve fauna, surpassed by the late Anisian fauna of the Leidapo Mb. (Tab. 1). Gastropods were on average the second most diverse taxon during the Early Triassic, and their increase in species richness during that time was comparable to that of bivalves. During the Middle Triassic, however, gastropod species richness increased more rapidly than bivalve species richness. In consequence, gastropods were the most diverse group in many Middle Triassic lithological units (Tab. 1). The change from the taxonomic dominance of bivalves in Early Triassic benthic communities to the taxonomic dominance of gastropods during the Middle Triassic can also be seen in the gastropod/bivalve-ratio that was variable but with an increasing trend through time (Fig. 14b). Brachiopods were the third most diverse group in almost all Early and Middle Triassic benthic

communities. Their species richness was relatively low during the Early Triassic, and in most Olenekian lithological units used for this comparison they are even not reported. However, brachiopods also became more diverse during the Middle Triassic, although their increase in species richness during the Middle Triassic is much slower compared to bivalves and gastropods.

The comparison between Early and Middle Triassic benthic communities confirms that corals were absent in the entire Early Triassic (e.g., Flügel 2002; Weidlich et al. 2003; Stanley 2003; Payne et al. 2006; Brayard et al. 2011). Sponges occurred only in two Lower Triassic formations used for this comparison, but sponges, in association with microbialites, are known from the Lower Triassic (Induan) of Armenia (Friesenbichler et al. 2018), Lower and Middle Triassic carbonate successions of the Western Tethys domain (the Alps, Carpathians and the Germanic Basin; Szulc 2007) as well as Lower Triassic strata from China (Ezaki et al. 2008; Bagherpour et al. 2017) and the Western US (Brayard et al. 2011; Hofmann et al. 2014). However, the number of these sponge species is not known. Middle Triassic sponges are not only reported in the lithological units shown in Tab. 1 but also in the Illyrian strata of the Wetterstein Fm. (Velledits et al. 2011). The fossil record of echinoderms in the Early to Middle Triassic is heterogeneous. Several Palaeozoic clades of echinoderms survived the end-Permian mass extinction and reappeared as Lazarus taxa in the Middle Triassic, without giving rise to a new diversification (Thuy et al. 2017). Crinoid diversity was very low during the Early Triassic (Hagdorn 2011), although cladistics analyses suggest that initial diversification took place in the Induan (Twitchett and Oji 2005) or already in the Late Permian (Oji and Twitchett (2015); however, well before the documented species richness increase during the Middle and early Late Triassic (Hagdorn 2011). Only two echinoid genera are reported from Lower Triassic strata (Twitchett and Oji 2005) and very low levels of diversity were apparently maintained for at least the duration of the Early and Middle Triassic. Nevertheless, numerous undescribed echinoid spines and other remains have been noted in Early Triassic fossil assemblages (e.g., from the Griesbachian of Oman; Krystyn et al. 2003) and these undescribed records may hint at a hidden diversity of echinoids within the Early Triassic (see also Thompson et al. 2015; Thuy et al. 2017). Fossil

remains or trace fossils attributed to Lower Triassic asteroids have only been recorded from Olenekian strata of the western USA (Schubert and Bottjer 1995; Villier et al. 2018). Definite reports from Lower Triassic holothuroids only exist from Western Nepal (Kozur and Mostler 1973; Mostler 1977), whereas a total number of 84 holothuroid species was reported from several Middle Triassic strata (Reich 2013). Fossil remains from ophiuroids are quite abundant in Lower Triassic strata worldwide but so far only six species have been described (Twitchett and Oji 2005). Early Triassic bryozoans were reported from a couple of Lower Triassic strata (Nakrem and Mørk 1991; Wignall and Twitchett 2002; Baud et al. 2008) but only five Early Triassic bryozoan genera are reported (Powers and Pachut 2007) and only six species have been described formally (Baud et al. 2008); however, bryozoan diversity increased during the Middle and Late Triassic, with eight reported genera (Powers and Pachut 2007) a total number of more than 40 species (see reviews in Schäfer and Grant-Mackie 1994; Schäfer et al. 2003). Microconchids were important constituents of marine ecosystems immediately after the Permian/Triassic mass extinction (He et al. 2012) and were also commonly present through the entire Early Triassic worldwide (Fraiser 2011; Zatoń et al. 2013b; Yang et al. 2015). Although microconchids can be very abundant locally, they are lowly diverse and only represented by three genera (Zatoń et al. 2013b).

The Middle Triassic increase in species richness might be related to more stable environmental conditions, as reflected by the constancy of the Middle Triassic carbon isotope curve (Payne et al. 2004), or alternatively represent the effect of competition-driven niche partitioning after rediversification exceeded a threshold (Hautmann 2014; Hautmann et al. 2015). The change in the gastropod/bivalve-ratio is more difficult to interpret, but it is notable that occurrences of high gastropod species richness relative to bivalves are almost exclusively linked to carbonate platform environments (Fig. 14b). This might represent a taphonomic bias due to differences in skeletal mineralogy between gastropods and bivalves, but we note that aragonite-shelled bivalves are commonly preserved in the Early Triassic, which makes this explanation unlikely. Alternatively, we hypothesise that the increase in gastropod species richness is a primary signal linked to the

resurgence of large carbonate platform and reefs during the Middle Triassic (Gaetani et al. 1981; Senowbari et al. 1993), although details of the ecological causes for this facies-related increase in gastropod species richness requires further investigation.

8. Conclusion

Early and Middle Triassic shallow-marine benthic communities differed considerably in terms of species richness and taxonomic composition. Whereas Early Triassic formations from shallow-marine settings contain generally less than 50 macroinvertebrate species, regional diversities of around 300 species have been described from various Anisian-Ladinian shallow-marine settings worldwide (Tab. 1; Fig. 14), including the herein studied fauna from the Pachycardientuffe. For more narrowly defined habitats, such as that of the open lagoon represented by the Schlernplateau fauna (85 species), the increase in diversity was likewise remarkable. The Middle Triassic increase in diversity at the local/regional level analysed herein correlates with the most pronounced increase in bivalve diversity during the entire Triassic in a global dataset (Hautmann 2007, fig. 8) and therefore represents the main phase of recovery after the end-Permian mass extinction. This main phase of recovery in benthic marine communities was associated with a weakening of the dominance of bivalves in comparison to the Early Triassic, which reflects the proliferation of other invertebrate taxa, particularly gastropods. We hypothesise that the resurgence of carbonate platforms during the Middle Triassic played an important role in the shift of taxonomic compositions, and that the increase of environmental diversity associated with newly arising carbonate platforms contributed at least partly to the accelerated pace of recovery during the Middle Triassic.

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Figure captions

Fig. 1 Locality map showing the position of the studied sections at the Seiser Alm/Alpe di Siusi (red stars) and the Schlern/Sciliar (blue stars). GPS-coordinates are N 46°30'40.8'', E 11°33'48.54'' for Schlern locality A and N 46°30'36.19'', E 11°33'51.9'' for Schlern locality B

Fig. 2 Field photographs. (a) Sampling locality Frommerbach A, showing the investigated section (see also Fig. 10 [left]). Scale = 1 m. (b) Sampling locality Frommerbach B, showing the investigated section (see also Fig. 10 [right]). (c) Western flank of the Seiser Klamm/Gola di Siusi showing the Schlernplateau beds (SchPl. beds), the post-volcanic bedded facies of the Rosszähne Fm. (RZ), volcanic rocks (V) and the pre-volcanic Schlerndolomite of the Rosengarten Fm. (R). The white rectangle indicates the position of (d). (d) Detailed look on the Schlernplateau beds. (e) Bioclastic rudstone from top of the Schlernplateau beds containing gastropods and bivalves. (f) Oncolites from the western Schlernplateau. Coin (16 mm) for scale

Fig. 3 Section of the Schlernplateau beds from the western flank of the Seiser Klamm/Gola di Siusi. M = marl, m = mudstone, w = wackestone, p = packstone, g = grainstone, SP = Schlernplateau. The Ladinian/Carnian boundary lies within bed SP10

Fig. 4 Rarefaction analyses from the Schlernplateau beds (a) and the Pachycardientuffe (b). Only samples with more than 40 individuals were analysed. See text for details. SP = Schlernplateau, SK = Seiser Klamm, SK-E = end of Seiser Klamm, FB = Frommmerbach

Fig. 5 Most common bivalves and gastropods collected at the Schlernplateau. (1) *Trigonodus costatus* von Wöhrmann and Koken, 1892, left valve interior (1A) and left valve exterior (1B), PZO5984, bed SP7. (2) *Cassianella bipartita* (von Klipstein, 1845), left valve, PZO5988, bed SP8. (3) *Entolioides zitteli* (von Wöhrmann and Koken, 1892), right valve, PZO5986. (4) *Myophoriopis richthofeni* (Stur, 1868), left valve, PZO5985, bed SP10. (5) *Myophoria kefersteini* (Münster in Goldfuss, 1837), left valve, PZO5987, bed SP8. (6) '*Loxonema*' *lineatum* von Wöhrmann and Koken, 1892, PZO5994, bed SP8. (7) '*Loxonema*' *aequale* von Wöhrmann and Koken, 1892, PZO5990, bed SP7. (8) *Stephanocosmia coronata* (von Wöhrmann and Koken, 1892), PZO5989. (9) *Zygopleura spinosa* von Wöhrmann and Koken, 1892, PZO5995bed SP8. (10) *Pustularia alpina* von Eichwald, 1851, PZO5998. (11) *Tretospira multistriata* von Wöhrmann and Koken, 1892, PZO5997, bed SP8. (12) *Coelostylina solida* (von Wöhrmann and Koken, 1892), PZO5996, bed SP7. (13) *Neritaria plicatilis* (von Klipstein, 1844), PZO5993, bed SP8. (14) *Naticopsis neritacea* (Münster, 1841), PZO5991, bed SP7. (15) *Palaeonarica concentrica* (Münster, 1841), PZO5992, bed SP7. Scale bars represent 1 cm for bivalves and 0.5 cm for gastropods

Fig. 6 Bivalves from the Pachycardientuffe. (1) *Pachycardia rugosa* von Hauer, 1857, right valve exterior (1A) and right valve interior (1B), PZO5980, bed FB B1. (2) *Heminajas fissidentata* (von Wöhrmann, 1889), left valve, PZO5983, bed FB A3. (3) *Pteria kokeni* (von Wöhrmann and Koken, 1892), left valve, PZO5982. (4) *Pachycardia plieningeri* Broili, 1903, left valve interior (4A) and left valve exterior (4B), PZO5981, bed FB B1. (5) *Myoconcha parvula* von Wöhrmann and Koken, 1892, right valve, SMNHS75537. (6) *Pteria salomoni* (Broili, 1903), right valve, SMNHS75534/1-2. (7) *Myoconcha curvata* Broili, 1903, left valve interior and left valve exterior, SMNHS10274. (8) *Mysidioptera interrupta* Broili, 1903, left valve, SMNHS17501/162. (9) *Trigonodus rablensis* (Gredler, 1862), right valve exterior (9A) and left valve interior (9B), 10284/1-3. (10) *Waagenoperna planata* (Broili, 1903), left valve, SMNHS17501/45. (11) *Mysidioptera emiliae* Bittner, 1900, right valve, SMNHS17501/12. (12) *Pteria tofanae* (Bittner, 1895), left valve, SMNHS75538, collected at

Tschapitbach. (13) *Newaagia lata* (von Klipstein, 1845), right valve interior, SMNHS75536. (14) *Parallelodon tschapitana* (Broili, 1903), right valve, SMNHS17501/250. Scale bars represent 1 cm

Fig. 7 Q-mode (samples) and R-mode (species) cluster analysis of samples with more than 40 individuals from the Schlernplateau beds using unweighted pair-group average and Morisita similarity index. The circle sizes represent the abundance of species within the corresponding sample (small circle = 1 individual, small medium-sized circle = 2-5 individuals, big medium-sized circle = 6-20 individuals, big circle = more than 20 individuals). SP = Schlernplateau, SK = Seiser Klamm, SK-E = end of Seiser Klamm. See text for details

Fig. 8 Rank-abundance distributions and guild-structures of the entire fauna of the Schlernplateau beds (a) and Pachycardientuffe (b). n = total number of individuals

Fig. 9 Rank-abundance distributions and guild-structures of representative fossiliferous beds SP14 (a), SP7 (b) and SP3 (c) from the Schlernplateau beds (see also Fig. 3). n = total number of individuals

Fig. 10 Sections Frommerbach A and B of the Pachycardientuffe from the Seiser Alm/Alpe di Siusi

Fig. 11 Rank-abundance distributions and guild-structures from the fossiliferous beds FB A3 (a), FB B2 (b) and FB B1 (c) from the Pachycardientuffe (see also Fig. 10). n = total number of individuals

Fig. 12 Lithological samples from locality Frommerbach A showing the highly fossiliferous limestone (a) and volcanoclastic sandy siltstone (b-c) containing disarticulated, randomly arranged bivalves. Scales are 23 mm (diameter of the coin) for (a) and 5 cm for (b) and (c)

Fig. 13 (a) Palaeoenvironmental reconstruction of the Schlern and Seiser Alm area during the Late Ladinian showing the distribution of sedimentary facies and the potential source areas of the Pachycardientuffe. (b) Panorama image taken from the top of the eastern margin of the Schlern mountain, showing present-day position of the former lagoon (Schlernplateau beds, 1), the post-volcanic reef (Rosszähne Fm., 2), the probable position of the suggested volcanic island (3) and the basin (Seiser Alm basin, Pachycardientuffe and Wengen Fm., 4)

Fig. 14 Diversity changes throughout the Early and Middle Triassic based on data shown in Tab. 1; see text for further explanation. (a) Total number of species. (b) Gastropod/bivalve-ratio. Blue lines mark formations with carbonate platform facies. G = Griesbachian; D = Dienerian; Sm = Smithian; Sp = Spathian, A = Aegean; B = Bithynian; P = Pelsonian; I = Illyrian; F = Fassanian; L = Longobardian; J = Julian; Carn. = Carnian; LT = Late Triassic. Marmolada = Marmolada Limestone; PachyT = Pachycardientuffe; Latemar = Latemar Limestone; SchPl = Schlernplateau beds

Table captions

Tab. 1 Benthic species richness of selected Early and Middle Triassic faunas. B = bivalves, G = gastropods, Br = brachiopods, C = corals, Sp = sponges, Cr = crinoids, E = echinoids, A = asteroids, Bry = bryozoans, Cru = crustaceans, H = holothurioids, M = microconchids, O = ophioroids, Pc = polychaete worms, Pp = polyplacophorans, Sc = scaphopods, ? = these taxa were reported but the exact number of species is unknown. Information about the age of the lithological units come from Fürsich and Wendt 1977, Broglio Loriga et al. 1990, Brack and Rieber 1993, Brack et al. 1996, Vörös 2003, Manfrin et al. 2005, Stiller and Bucher 2008, Hagdorn and Nitsch 2009, Shigeta et al. 2009, Balini et al. 2010, Hofmann et al. 2013a, 2013b, 2014, 2015, Urlichs 2014, Foster et al. 2015, 2017, Hausmann and Nützel 2015, Hautmann et al. 2015, Brayard et al. 2017, Foster and Sebe 2017. See text for details

Online Resources captions

Online Resource 1 Excel tables showing the quantitative matrix of fossil occurrences used for data analyses, the comparison between the faunas of the Schlernplateau beds and the Pachycardientuffe as well as the number of species, number of individuals and Simpson-D values for each fossiliferous bed

Revision notes

Ref.: Ms. No. PAZE-D-17-00052R1

Palaeoecology of Late Ladinian (Middle Triassic) benthic faunas from the Schlern/Sciliar and Seiser Alm/Alpe di Siusi area (South Tyrol, Italy)

General note: Please see attached document with "track changes" for the details of our changes in response to the reviewer's comments.

Reviewer's comments

AUTHOR AFFILIATIONS:

Once again, to avoid any confusion, please please split the affiliations of Alexander Nützel ... SNSB-BSPG and LMU are clearly different institutions (see my former comments)

Response: We split the affiliation of Alexander Nützel and apologize that we did not do that in the first place.

TEXT:

Page 22, line 505 ... Szulc INSTEAD OF Sculz 2007

Page 23, line 524 ... Kozur and Mostler 1973 IS MISSING in your REFERENCES

Page 23, lines 524/525 ... Mostler 1977 IS MISSING in your REFERENCES

Page 23, line 526 ... Reich 2013 IS MISSING in your REFERENCES

Page 24, line 548 ... Gaetani et al. 1981 INSTEAD OF Gaetani 1981

Page 28, line 646 ... Eichwald, E. von. 1851. INSTEAD OF Eichwald, M. 1851.

Page 28, line 646 ... Geognosie, auf INSTEAD OF Geognosie auf

Page 28, line 647 ... die Eifel, Tyrol, Italien, Sizilien INSTEAD OF die Eife, Tirol, Sizilien

Page 30, line 691 ... Gümbel, C.W. 1861. INSTEAD OF Gümbel, C.W. von 1861. ...(Gümbel was nobled in 1882)

Page 33, lines 754/55 ... implement Kozur and Mostler 1973 (see Page 23, line 524)

Page 34, lines 782/783 ... implement Mostler 1977 (see Page 23, lines 524/525)

Page 36, lines 820/821 ... implement Reich 2013 (see Page 23, line 526)

Page 36, lines 825-826 ... DELETE Sano and Nakashima 1997 which is not cited in text etc.

Page 39, line 887 ... "Trachyceras" IN ITALICS please

Page 39, line 889 ... "Myophoria kefersteini" IN ITALICS please

Page 40, line 928 ... Yin INSTEAD OF Ying

Page 41, line 930 ... Yin INSTEAD OF Ying

Page 41, line 932 ... Yin INSTEAD OF Ying

Page 43 ... line 981 ... von Eichwald, 1851 INSTEAD OF Eichwald, 1851

Response: As requested we changed the above mentioned text passages and deleted the work of Sano and Nakazawa (1997). Naturally, we added the work of Kozur and Mostler (1973), Mostler (1977) and Reich (2013) to the reference list and apologize that this mistake did not track our attention before.

REFERENCES:

Please check again my former comments (comment 5) ... Please use an en-dash NOT a hyphen netween page numbers

Response: All hyphens between page numbers were changed into en-dashes.

TABLE:

Frizzell and Exline (1956) INSTEAD OF Frizzell and Exline (1955)

Response: We changed the above mentioned text passage as requested.

ONLINE RESOURCE:

Please re-format your species names ... "sp.", "sp. 1...", "cf.", "n.sp." NOT IN ITALICS

Response: We performed the necessary changes in our electronic supplementary material.

Further changes

Independently from the reviewer's suggestions we performed some minor changes on the manuscript, which can be seen in the track-edited version of the manuscript.

Palaeoecology of Late Ladinian (Middle Triassic) benthic faunas from the Schlern/Sciliar and Seiser Alm/Alpe di Siusi area (South Tyrol, Italy)

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22 benefited from careful reviews by William Foster, Christopher A. McRoberts, Simon Schneider and
23 Mike Reich.

Abstract

The Schlern and Seiser Alm area (South Tyrol, Italy) is a classical locality for studies of Middle Triassic platform to basin transitions, yet details of the palaeoecology of the rich benthic faunas of this area have been insufficiently known. We herein present a detailed palaeoecological study of the fauna from the Schlernplateau beds (late Ladinian to early Carnian) and the more or less time-equivalent Pachycardientuffe (late Ladinian), which is based on quantitative faunal data. The palaeoecology as well as sedimentary features suggest that the fauna of the Schlernplateau beds represents a lagoonal soft bottom fauna. The high species richness of the fauna as well as the locally restricted occurrences of fossils indicate an open lagoonal setting palaeogeographically close to an oceanic inlet. The high evenness of the fauna is probably a result of time-averaging. In contrast, the fauna of the Pachycardientuffe shows clear indications of transportation. Ecological features of this fauna and palaeogeographic reconstructions suggest three potential source areas: (1) the lagoon represented by the Schlernplateau beds, (2) the reef fringing this lagoon and (3) a shallow clastic coast of a nearby volcanic island and/or submarine high. A comparison between diversities of selected Early and Middle Triassic lithological units revealed the increasing species richness of all major benthic taxa during the Middle Triassic and a shift from bivalve dominated Early Triassic faunas to gastropod dominated faunas.

Keywords: Middle Triassic, biotic recovery, quantitative faunal analyses, palaeoecology, palaeoenvironment.

Kurzfassung

Obwohl das Gebiet des Schlern und der Seiser Alm (Südtirol, Italien) seit langem als klassische Lokalität für die Erforschung mitteltriassischer Plattform-Becken-Übergänge gilt, ist die Paläoökologie ihrer reichen benthischen Fauna unzureichend erforscht. Wir präsentieren eine detaillierte paläoökologische Studie der Fauna der Schlernplateau-Schichten (spätes Ladinium bis frühes Karnium) und der mehr oder weniger gleichalten Pachycardientuffe (spätes Ladinium), welche auf quantitativen Daten basiert. Die Paläoökologie sowie der sedimentologische Kontext legen nahe, dass die Fauna der Schlernplateau-Schichten eine lagunäre Weichbodenfauna repräsentiert. Ihre hohe Diversität sowie die lokal begrenzten Vorkommen der Fossilien deuten auf eine offene Lagune hin, die sich paläogeographisch nahe an einem Einlass zum offenen Meer befand. Die hohe Gleichmäßigkeit der Fauna ist höchstwahrscheinlich das Resultat von „time-averaging“. Im Gegensatz dazu gibt es in der Fauna der Pachycardientuffe klare Hinweise auf Transport. Die Ökologie dieser Fauna und paläogeographische Rekonstruktionen lassen auf drei potentielle Herkunftsgebiete schließen: (1) die Lagune, welche durch die Schlernplateau-Schichten repräsentiert wird, (2) das Saumriff dieser Lagune und (3) eine flache, siliziklastische Küste nahe einer vulkanischen Insel und/oder einer submarinen Hochzone. Ein Vergleich der Diversitäten ausgewählter früh- und mitteltriassischer lithologischer Einheiten offenbart einen Anstieg der Diversität während der Früh- und Mitteltrias sowie einen Wechsel von Muschel-dominierten frühtriassischen Faunen zu Gastropoden-dominierten Faunen während der Mitteltrias.

Schlüsselwörter: Mitteltrias, ökologische Erholung, quantitative Faunen-Analysen, Paläoökologie, Paläo-Umwelt.

1. Introduction

72 The recovery from the end-Permian mass extinction, which killed between 81% (Stanley 2016)
73 and 96% (Raup 1979) of marine species, provides a unique test-case for studying long-term
74 evolutionary responses to a sudden and massive loss of species on a global scale. Scientific interest in
75 studying the recovery pattern is twofold: it allows testing macroevolutionary models (e.g., Brayard et
76 al. 2009; Hautmann et al. 2015), and it represents a (pessimistic) analogue for the long-term future of
77 biosphere in the face of anthropogenically caused environmental changes (Payne and Clapham
78 2012).

79 Understanding evolutionary processes requires the study of species in their ecological context.
80 Concerning the recovery from the end-Permian mass extinction, much palaeoecological work has
81 been done in the past decades, but these studies almost exclusively concentrated on the Early
82 Triassic (e.g., Schubert and Bottjer 1995; Twitchett and Wignall 1996; Hofmann et al. 2013a, 2013b,
83 2014, 2015; Hautmann et al. 2011, 2015; Foster et al. 2017), which is the ca. 4 Ma time interval that
84 followed the end-Permian mass extinction. However, biodiversity in terms of global taxonomic
85 richness did not reach the pre-extinction level before the Late Jurassic (Sepkoski 1997) or later (Alroy
86 et al. 2008). With regard to alpha-diversity in local environments, the major recovery step seems to
87 have taken place during the Middle Triassic, as evidenced by the striking differences between most
88 diverse Early Triassic communities that include around 45 benthic species (Hautmann et al. 2013,
89 2015; Hofmann et al. 2013b, 2014) and, e.g., the hyperdiversified fauna from the Longobardian–
90 Julian (Late Ladinian–Early Carnian) Cassian Fm. of northern Italy (>1000 benthic species; Tab. 1). The
91 progress in recovery during the Middle Triassic has been addressed in several recent studies (e.g.,
92 Payne 2005; Payne et al. 2006; Song et al. 2011; Velledits et al. 2011; Foster and Sebe 2017) but data
93 are still relatively scarce.

94 This study is based on quantitative bed-rock sampling in the area of Schlern/Sciliar mountain and
95 Seiser Alm/Alpe di Siusi (South Tyrol, Italy; Fig. 1), which is a paradigm for a Middle to Late Triassic
96 reef-to-basin landscape. It is one of the few places in the world where the platform-slope-basin
97 transitional zone is preserved in its primary setting (Keim 2008; Brandner et al. 2016), giving the

opportunity to study the ecology of concurrent faunas in different environments. Sampling was carried out (1) in sediments of a lagoonal setting represented by the locally highly fossiliferous Schlernplateau beds on the Schlern mountain and (2) in the basinal setting of the 'Pachycardientuffe' at the Seiser Alm, which represent approximately the same stratigraphic age (see chapter 3). The palaeoecology and species distributions of both faunas are discussed in the context of their depositional environments, and their diversities are compared with published data on Early–Middle Triassic benthic communities from other regions, which allows preliminary insights into diversity changes through the Early and Middle Triassic time interval.

2. Material and Methods

Fieldwork was carried out in August 2016 at the Seiser Alm/Alpe di Siusi and the Schlern/Sciliar mountain in South Tyrol/Alto Adige in northern Italy. At the Seiser Alm, fossils were sampled in the gorge of the Frommerbach/Rio Frommer and one of its eastern tributaries (Figs 1 and 2a-b). On the Schlern, fossils were mainly collected on the western flank of the Seiser Klamm/Gola di Siusi (Figs 1 and 2c-d). Outcropping rock material of fossiliferous beds was quantitatively sampled until the occurrences of fossils were exhausted. Additionally, fossils quantitatively collected by M. Urlichs between 1998 and 2012 at the same localities were included in the analyses. Specimens used for the palaeoecological analyses are housed at the State Museum of Natural History Stuttgart (Germany, inventory numbers SMNHS17501/250 - SMNHS75538) and the Museum of Nature South Tyrol (Italy, inventory numbers PZO5980 - PZO5998). For taxonomic identification fossils were first washed and then, when necessary, prepared with micro jacks. A quantitative matrix of fossil occurrences was compiled at species level (Online Resource 1). For bivalves, the number of individuals has been inferred by counting only the most numerous valves (left or right) together with articulated specimens. Only fossils that (1) were clearly relatable to specific beds of the investigated outcrops

and (2) samples with more than 40 individuals were used for palaeoecological data analyses. Sedimentological observations in the field and information from ecological analyses were used for the interpretation of the depositional environment. Our complete dataset comprises 2723 individuals assigned to 53 species for the Schlernplateau beds and 651 individuals assigned to 59 species for the Pachycardientuffe.

Ecological parameters and statistical analyses were calculated using the software PAST, version 2.17 (Hammer et al. 2001). Based on the species-abundance data, rarefaction analyses were carried out for each sample in order to compare species richness of faunas with different sample sizes and to assess the relative completeness of sampling. For further ecological characterization, rank-abundance distributions, trophic nuclei, and ecological pie charts were used. The trophic nucleus of an association comprises those species that contribute 80% of the total number of individuals in an association (Neyman 1967). Following Aberhan (1994), species were assigned to 10 trophic guilds, based on functional morphology, mode of life of related Recent species, information from the literature, and the sedimentological context. Gastropods were collectively assigned to epifaunal herbivores and/or detritus-feeders, since evidence for more specialized feeding lacks. For the identification of recurrent assemblages and groups of ecologically related species, Q-mode cluster analyses were calculated for samples containing more than 40 individuals, using the Morisita similarity index (Morisita 1959) and unweighted pair-group average. Additionally, R-mode cluster analyses were used for the identification of sets of species that typically co-occur.

3. Geologic setting

The Schlern and the adjacent Rosengarten/Catinaccio represent a Middle Triassic carbonate platform with northeastward, eastward to southeastward inclined reef slopes (Brandner 1991;

147 Bosellini 1998; Brandner et al. 2007; Keim 2008). Towards the west, there was probably a connection
148 to the Mendel platform (Keim 2008). The Schlern Mountain is build up by (1) the pre-volcanic, up to
149 800 m thick 'Schlerndolomite' (Rosengarten Fm.), (2) up to 40 m thick volcanic rocks and (3) post-
150 volcanic, well-bedded dolomite formerly known as 'Rosetta Dolomite' or 'Cassian Dolomite', now
151 interpreted as the platform facies of the Rosszähne Fm. The latter is overlain by (4) the
152 Schlernplateau beds, which is a sequence of carbonate rocks and grey to reddish marls that are
153 locally highly fossiliferous and commonly interpreted as lagoonal sediments (Figs 2c-d; Keim 2008;
154 Brandner et al. 2016). Findings of the biostratigraphically important ammonoid *Prototrachyceras*
155 *archelaus* (Laube, 1869b) indicate a Late Ladinian age of the Schlernplateau beds (Brandner 1991;
156 Urlichs and Tichy 2000). However, the occurrence of the bivalve *Myophoria kefersteini kefersteini*
157 (Münster in Goldfuss, 1837) in the uppermost 6 m of the Schlernplateau beds suggests that the top
158 of the formation extends into the Lower Carnian (Urlichs 2014). The thickness of the Schlernplateau
159 beds varies from only a few meters to a maximum of ca. 40 m. Towards the platform margins, the
160 Schlernplateau beds interfinger with the reef flat facies.

161 During deposition of the Rosszähne Fm. and Schlernplateau beds at the top of the Schlern
162 carbonate platform, the adjacent Seiser Alm basin was filled with a more than 500 m thick
163 successions of volcanoclastic detritus of the Wengen Fm. and, later, the mixed siliciclastic-carbonate
164 succession of the St. Cassian/San Cassiano Fm. (Brandner 1991). Within the Wengen Fm. of the Seiser
165 Alm, the Late Ladinian (Urlichs 1977, 1994, 2014) 'Pachycardientuffe', which are named for the mass
166 occurrence of the bivalve *Pachycardia rugosa* von Hauer, 1857, represent several (at least two)
167 conglomeratic, highly fossiliferous intercalations that have been mapped as distal parts of the
168 'Marmolada Conglomerate' in the geological map of the western Dolomites (Autonome Provinz
169 Bozen (ed.) 2007). However, the Marmolada Conglomerate in the strict sense is a volcanogenic
170 conglomerate that was transported from a source area near the Marmolada Mountain (ca. 20 km
171 east of the study area) into adjacent basins (e.g., Bosellini 1998; Bottoli and Trombetta 1998). In
172 contrast, the lithology of the Pachycardientuffe is dominated by non-dolomitized limestone pebbles

and cobbles (small to medium sized 'Cipit boulders') that originate from adjacent carbonate platforms. We therefore assume that the Pachycardientuffe represent distal equivalents of tongues of foreslope talus deposits, as described by Yose (1991) in a proximal facies at the Mahlknecht cliff, around 4 km SE of our sampling localities. The admixed volcanogenic pebbles and volcanoclastic matrix could either have been taken up during transportation, or stem from a second source area, or could represent the result of mixing of carbonate and volcanogenic components by reworking (see chapter 5.2.).

4. The Schlernplateau beds

Early workers erroneously correlated the fauna of the Schlernplateau beds with the younger Raibl Fm. (Carnian), based among other reasons on the occurrence of *Myophoria kefersteini* (Münster in Goldfuss, 1837; e.g., von Richthofen 1860). This view was also shared by von Wöhrmann and Koken (1892) in their comprehensive description of the Schlernplateau fauna and was maintained by most subsequent authors until Brandner (1991), Urlichs and Tichy (2000) and Urlichs (2014) provided evidence for a Late Ladinian (*Prototrachyceras archelarus–Frankites regoledanus* ammonoid zone) to early Carnian (*Daxatina canadensis* ammonoid zone) age. In addition to ammonoid finds, the key observation for the revised stratigraphy was the existence of several subspecies of *Myophoria kefersteini*, which are indicative of different stratigraphic intervals (Urlichs 2014). With this updated stratigraphic information, Schlernplateau beds and Pachycardientuffe are more or less time-equivalent units.

Von Wöhrmann and Koken (1892) described 72 species, including 33 gastropod species, 24 bivalve species, eight cephalopod species, three echinoid species, two coral species and one crinoid species from the Schlernplateau beds. Notably, nearly all specimens of this rich fauna stem from a

197 limited area at the western flank and southern part of the Seiser Klamm. The only other locality that
198 is explicitly mentioned in von Wöhrmann and Koken (1892) is the 'Burgstall', some hundred meters
199 east of the Seiser Klamm, where one coral species (*Thecosmilia rothpletzi* von Wöhrmann and Koken,
200 1892), fragments of crinoids and echinoid spines were found. Our survey confirms that fossils are
201 scarce or absent at other places of the Schlernplateau. At the Seiser Klamm locality, fossils are most
202 abundant in the upper part of the section, particularly in several layers of red marl (Fig. 3). Fossils are
203 also abundant in several rudstone beds near the top of the section (Fig. 2e), but the crystallized
204 limestone makes it difficult to extract them from the matrix.

205 A detailed section was measured at the western flank of the Seiser Klamm and samples were
206 taken from three localities on the Maultierrücken/Dorsale del Mul (Figs 1 and 3). The investigated
207 section starts with an alternation (ca. 20 m) of partly dolomitic limestone beds, which are separated
208 by marls or covered intervals that probably also represent fine-grained sediments. The limestone and
209 dolomite beds are mud-, wacke-, pack- and grainstones that sometimes contain bioclasts like bivalve
210 and gastropod shells and, less common, ooids. The overlaying marl beds (SP3 and SP5) are highly
211 fossiliferous. Above these marls, an around 3 m thick sequence of thick-bedded wackestone forms a
212 prominent cliff, the top of which is formed by a 30 cm thick oolitic limestone bed (at a height of 25
213 m). Several marly, highly fossiliferous intervals above this cliff provided the majority of fossils studied
214 herein. Within the marly intervals, laterally discontinuous oolithic limestone beds are repeatedly
215 intercalated, which sometimes contain bioclasts such as gastropod and bivalve shells. A notable
216 lithological marker bed near the top of the section contains shell debris, ooids, and interspersed
217 pisolithic iron ore grains. Surface ornamentations on the fossils are generally well preserved. This lack
218 of abrasion as well as the fact that some bivalves were preserved with conjoined valves indicate that
219 the fossils were not transported over larger distances. According to Urlichs and Tichy (2000) and
220 Urlichs (2014) the uppermost layers of the investigated section are already Carnian in age.
221 Accordingly, the Ladinian/Carnian boundary lies within fossiliferous bed SP10 (Fig. 3).

222

4.1. Fauna of the Schlernplateau beds

A total number of 53 species occurring in 16 fossiliferous beds (SP1-SP16, Fig. 3) was identified, including 27 gastropod species, 19 bivalve species, four coral species and one sponge species (Online Resource 1). Notably, brachiopods are absent, and only one crinoid columnal fragment and one echinoid spine were found. In terms of species richness, our collection is comparable to the diversity described in the monograph of von Wöhrmann and Koken (1892; 72 species). Species richness within the different beds varies between 2 to 32. However, rarefaction analyses of samples from each fossil horizon indicate different degrees of sampling completeness (Fig. 4a).

The 10 most frequent species are, in descending order, *Myophoria kefersteini* (Münster in Goldfuss, 1837) (bivalve, 16.3%), *Heminajas fissidentata* (von Wöhrmann, 1889) (bivalve, 11.4%), *Pachycardia rugosa* von Hauer, 1857 (bivalve, 9.7%), *Neritaria plicatilis* (von Klipstein, 1844) (gastropod, 8.3%), *Naticopsis neritacea* (Münster, 1841) (gastropod, 8%), *Coelostylina solida* (von Wöhrmann and Koken, 1892) (gastropod, 5.8%), *Palaeonarica concentrica* (Münster, 1841) (gastropod, 4.3%), *Myophoriopis richthofeni* (Stur, 1868) (bivalve, 4%), *Trigonodus rablensis* (Gredler, 1862) (bivalve, 3.8%) and '*Loxonema*' *aequale* von Wöhrmann and Koken, 1892 (gastropod, 3.3%). These 10 species together with *Cassianella bipartita* (von Klipstein, 1845) (bivalve, 3.2%) and *Stephanocosmia coronata* (von Wöhrmann and Koken, 1892) (gastropod, 3%; Fig. 5 and 6) constitute the trophic nucleus of the complete fauna at the Schlernplateau. Simpson's index of dominance of associations from different fossiliferous beds is generally high and varies between 0.06 and 0.30, with an average value of 0.2 (Online Resource 1).

Cluster analysis (Fig. 7) did not reveal the existence of clearly distinct associations. However, a cluster of samples that are dominated by *Myophoria kefersteini* is set off from samples in which species of *Pachycardia* and *Trigonodus* are more abundant. Because *Myophoria*, *Trigonodus* and *Pachycardia* are not only phylogenetically closely related but also ecologically similar (both are

248 shallow infaunal suspension feeders), we do not believe that these two clusters represent
249 fundamentally different environmental conditions. As an alternative explanation, it seems possible
250 that haphazardness of larvae settlement had randomly favoured different dominant species at
251 different times.

252 Although the fauna of the Schlernplateau beds is gastropod dominated in terms of species
253 richness, it is bivalve dominated in terms of total number of individuals. Accordingly, most species
254 were epifaunal herbivores and/or detritus-feeders, whereas almost half of all collected individuals
255 are shallow infaunal suspension-feeders, followed by epifaunal herbivores and/or detritus-feeders
256 and free-lying epifaunal suspension-feeders (Fig. 8a). However, the guild-specific diversity and
257 absolute abundance of trophic guilds can vary between different fossiliferous beds (Fig. 9).

258 Frequency distributions of assemblages from different fossiliferous beds show different patterns,
259 but a remarkable aspect is that many show an unusually high degree of evenness (Figs 9b-c). The lack
260 of abrasion, occurrence of bivalves with conjoined valves, and the sedimentological context
261 (occurrence in fine-grained sediments) exclude that this pattern is due to effects of faunal mixing by
262 transportation. Another notable aspect is that there are often lateral differences in the faunal
263 composition within single fossiliferous beds (Fig. 9).

264

265 **4.2. Interpretation of the Schlernplateau fauna**

266

267 The geologic context leaves little doubt that the Schlernplateau beds represent lagoonal
268 sediments of the platform interior. This is evident by the sedimentary features of the Schlernplateau
269 beds themselves, which include the coexistence of high- and low-energy sediments (e.g., oolites and
270 shell coquinas (rudstones) versus marls, wackestones, and early diagenetic dolomites) and the
271 presence of locally abundant oncoids (Fig. 2f). It is further corroborated by the lateral facies change,
272 which includes the transition to fringing coral reefs on the supposed seaward side and to pedogenic

sediments at places where the platform was emerged (Brandner et al. 2016 and own observations). Finally, the ecology of the documented fauna is in accordance with a lagoonal setting because shallow infaunal suspension-feeders and free-lying epifaunal suspension-feeders dominate, which are commonly associated with a soft substratum.

Given the lagoonal setting, two aspects of the Schlernplateau fauna are remarkable. First, the species richness is unusually high for this environment. Although decidedly stenohaline organisms lack (e.g., brachiopods) or are extremely rare (e.g., echinoderms and ammonoids), the high species richness excludes that the lagoon was (at the place where the samples were taken) affected by high environmental stress such as changing salinity, which often characterizes restricted lagoons (e.g., Fürsich 1994; Fürsich et al. 1995). The second unusual aspect is the extremely high evenness in many samples. Based on the state of preservation and the occurrence in marly beds (see above), faunal mixing by transportation can be excluded. However, no examples of primary causes for such high evenness are known to us from ecologically comparable faunas. We therefore assume that the high evenness may, at least partly, reflect the effects of time-averaging. Fürsich and Aberhan (1990) nicely demonstrated how time-averaging may produce abundance patterns similar to those that we observed in the Schlernplateau beds.

Our summary interpretation of the sedimentological and faunistic data is that the Schlernplateau beds represent an open lagoon and that the outcrop area around the Seiser Klamm was palaeogeographically close to an oceanic inlet that prevented large-scale fluctuations in salinity and temperature, provided supply of food for filter feeding organisms, and was the source of larvae that settled within the lagoon. The randomness in the composition of larvae that reached the lagoon may be partly responsible for differences in the faunal composition. In this model, successive communities went back to different settlement events, each with a particular taxonomic composition of larvae and thus resulting in different dominance of the resulting cohort. Superimposition of abundance patterns of successive communities by time-averaging then caused a pattern where many species are nearly equally abundant. However, prevalent species probably dominated at different

299 times. We note that time-averaging might have also contributed to the high overall species richness,
300 but even if this effect is considered, the Schlernplateau beds are still remarkably species rich.

301 Additional support for the open lagoon model comes from the fact that fossil occurrences are
302 locally restricted (close to oceanic inlets in our interpretation). From a sedimentological perspective,
303 the laterally discontinuous oolitic limestone beds that are intercalated in the low-energy marls
304 probably represent washover deposits from a nearby barrier, which however was discontinuous near
305 the fossil locality.

306

307 **5. The Pachycardientuffe/Tufi a Pachycardie**

308

309 Like the fauna from the Schlernplateau beds, the highly diverse fauna of the Pachycardientuffe is
310 known for more than 100 years. Broili (1903) described 157 species, including 122 bivalve species, 18
311 brachiopod species, 13 echinoid species and four crinoid species. Blaschke (1905) added the
312 description of 77 gastropod species, as well as three sponge species, five coral species, one
313 scaphopod species and 14 bivalve species that were not described in Broili (1903). A detailed
314 description of brachiopods from the Pachycardientuffe was given by Waagen (1903). After a revision
315 by Waagen (1907) a total number of 165 bivalve species is described from the Pachycardientuffe.
316 Overall, more than 270 species have been reported from the Pachycardientuffe thus far (Tab. 1). It
317 should be noted, however, that some of the major fossil localities (e.g., at the Tschapitbach/Rio Cipit)
318 are currently covered and therefore not accessible.

319 The investigated section at locality Frommerbach A is located in the gorge of the Frommerbach
320 itself (Figs 1, 2a and 10). It starts with a fossiliferous conglomerate at 1850 m altitude that overlies
321 volcanoclastic sandstone beds of the Wengen Fm. with an erosional disconformity. The pebbles are
322 mainly limestones and less commonly rounded volcanic rocks, which are embedded in a siltstone

matrix. The overlaying bedded sandstone contains limestone blocks at its top. The components of the following fossiliferous conglomerate consist of limestone and volcanoclastics. After a 3 m thick interval of siltstone, highly fossiliferous sandy siltstones follow on top of this section. The investigated section Frommerbach B is located in an eastern tributary of the Frommerbach (Figs 1, 2b and 10) at 1850 m altitude. The rocks are matrix supported, fossiliferous, pebble bearing, volcanogenic, middle- to coarse grained sandstones. As pointed out by Urlichs (2014), the fossiliferous rocks in the two Frommerbach sections do not belong to the same horizon. The investigated rocks of section Frommerbach A are younger than the rocks from Frommerbach B. For a detailed stratigraphic correlation between the sections see Fig. 3 in Urlichs (2014).

5.1. Fauna of the Pachycardientuffe

At the two Frommerbach localities a total number of 59 species was found, which is much less than the overall species richness of the Pachycardientuffe (277 species), as described in Broili (1903), Waagen (1903), Blaschke (1905) and Waagen (1907). These 59 species include 30 bivalve species, 16 gastropod species, five echinoid species, three coral species, three crinoid species and two brachiopod species. Sponges are absent. The seven most frequent species are, in descending order, *Pachycardia rugosa* von Hauer, 1857 (54.4%), *Pachycardia plieningeri* Broili, 1903 (27.3%), *Trigonodus rablensis* (Gredler, 1862) (3.7%), *Myophoria kefersteini* (Münster in Goldfuss, 1837) (1.8%), *Fedaiella inaequiplicata* (von Klipstein, 1843) (gastropod, 1.4%), *Naticopsis seisiensis* (Blaschke, 1905) (gastropod 1.2%) and *Heminajas fissidentata* (von Wöhrmann, 1889) (1.1%; Figs 5 and 6). The fauna is clearly dominated by the two bivalve species *Pachycardia rugosa* and *Pachycardia plieningeri* that form the trophic nucleus. All other species are relatively rare and almost half of the species is only represented by one individual (Figs 8b and 11). Simpson-D ranges between

347 0.29 and 0.47, with an average value of 0.39 (Online Resource 1). Again, the rarefaction analysis
348 shows that the diversity of some samples is underestimated (Fig. 4b).

349 A palaeontological analysis of the fauna from the Pachycardientuffe was already performed by
350 Fürsich and Wendt (1977), based on 283 individuals belonging to 26 species, including bivalves (11
351 species), gastropods (11 species), crinoids (two species), echinoids and corals (one species,
352 respectively). This analysis shows a similar rank-abundance pattern as in our study. *Pachycardia*
353 *rugosa* is with 85.5% the most abundant species, whereas almost three-quarters of all species are
354 represented by only one individual. Because Fürsich and Wendt (1977) did not separate *Pachycardia*
355 *rugosa* and *Pachycardia plieningeri*, the Simpson-D in their study is relatively higher (0.71) than in our
356 study (min. D = 0.29; max. D = 0.46). Whether *P. rugosa* and *P. plieningeri* represent two different
357 species is debatable. In this study, we used the less deeply depressed lunule and the more posterior
358 position of the beaks in *P. plieningeri* as criteria for their separation. Additional criteria noted by
359 Broili (1903) include a more elongated outline and more elongated, but narrower anterior cardinal
360 tooth in *P. plieningeri*.

361 The fauna of the Pachycardientuffe is bivalve dominated in terms of species richness and total
362 number of individuals. The guild-species diversity shows that epifaunal herbivores and/or detritus-
363 feeders, epibyssate suspension-feeders and shallow infaunal suspension-feeders are the most
364 important guilds (Fig. 8b). However, most individuals belong to shallow to moderate deep infaunal
365 suspension-feeders, which is not surprising since both dominating species belong to this group.

366

367 **5.2. Interpretation of the fauna from the Pachycardientuffe**

368

369 Several lines of evidence indicate that the fauna of the Pachycardientuffe is allochthonous: (1) the
370 lack of fossils that were preserved in life position; (2) the lack of bivalves that are preserved with

371 conjoined valves; (3) frequent fragmentation of fossils; (4) the poorly sorted sediment. These
372 observations raise the question where the transported fossils originally came from.

373 In contrast to the Schlernplateau fauna, where many species occur in similar abundances, the
374 fauna from the Pachycardientuffe is clearly dominated by only two species, namely *Pachycardia*
375 *rugosa* and *Pachycardia plieningeri*. A comparison between the fauna of the Schlernplateau beds and
376 the Pachycardientuffe revealed that 45% of all species occur exclusively in the Pachycardientuffe and
377 38% of all species occur exclusively in the Schlernplateau beds. The remaining 17% of all species
378 occur in the Schlernplateau beds as well as in the Pachycardientuffe (Online Resource 1). Species that
379 occur in the Schlernplateau beds as well as in the Pachycardientuffe include the bivalve species
380 *Myophoria kefersteini*, *Heminajas fissidentata*, *Pachycardia rugosa*, *Myophoriopis richthofeni* and
381 *Trigonodus rablensis*, which belong to the most abundant species in the Schlernplateau beds as well
382 as in the Pachycardientuffe. All these species were shallow infaunal suspension-feeders that required
383 a soft substratum. However, there are large differences in the relative abundances of these species
384 between the Schlernplateau beds and the Pachycardientuffe. *Myophoria kefersteini* and *Heminajas*
385 *fissidentata* are the most common species in the Schlernplateau beds but only occur rarely in the
386 Pachycardientuffe. In contrast, *Pachycardia rugosa* is the dominant species in the Pachycardientuffe,
387 but it ranks third in the Schlernplateau beds, where it is much less common than *Myophoria*
388 *kefersteini* and *Heminajas fissidentata*. If the Schlernplateau beds were the only source area for the
389 fossils of the Pachycardientuffe, then *Pachycardia rugosa* should be less dominant. It is therefore
390 likely that the fauna of the Pachycardientuffe did not originate solely from the Schlernplateau beds.

391 Based on palaeogeographic reconstructions (Brandner 1991, p. 12, Fig. 6; own observations) and
392 ecological features of the fauna, we identified two additional possible source areas for the fauna of
393 the Pachycardientuffe. One of these additional source areas is the shallow clastic coast of a nearby
394 volcanic island and/or adjacent submarine highs, where a fauna could have flourished in
395 volcanoclastic sediments. Brandner (1991, p. 12, Fig. 6) indicated the presence of a structural high
396 with a volcanic island topography few kilometres southeast of the Frommerbach localities, which was

397 caused by the tectonic activity during the Late Ladinian and consisted of uplifted volcanoclastics of
398 the Wengen Fm. Thick shelled, shallow-burrowing bivalves such as *Pachycardia* are typical faunal
399 elements of such shallow-marine, sandy sediments (Stanley 1970). Brandner (1991, p. 12, Fig. 6)
400 indicated dipping of the palaeo-relief of the structural high towards the northwest, directly pointing
401 towards the Frommerbach localities (see also Yose 1991, p. 35). We assume that at least parts of the
402 fauna of the Pachycardientuffe were transported from this source area via submarine high-density
403 gravity flows, together with volcanogenic material (Figs 12a-c). A similar scenario was already
404 described by Fürsich and Wendt (1977), who assumed that the high number of *Pachycardia* indicates
405 a distinct association in a shallow-water high-energy environment, e.g. in the vicinity of volcanic
406 swells or islands, and that this *Pachycardia* dominated fauna together with tuffitic material and
407 faunal elements from neighbouring biotopes was transported into the basin.

408 A third possible source area is the reef environment that fringed the lagoon of the Schlernplateau
409 beds. Blaschke (1905, p. 219) reported the presence of several bivalve taxa in the Pachycardientuffe
410 that have previously been reported from the reefal facies of the "Schlerndolomit" *sensu lato*. These
411 bivalves include *Chlamys* (*Granulochlamys*) cf. *tubulifera* (Münster, 1841), *Mysidioptera* cf.
412 *aviculaeformis* Broili, 1903, *Mysidioptera* cf. *incurvostriata* (Gümbel, 1861), *Mysidioptera* cf. *spinigera*
413 Bittner, 1895, *Mysidioptera acuta* Broili, 1903, *Mysidioptera* cf. *laczkói* Bittner, 1901, *Cassianella*
414 *decussata* (Münster, 1841), *Waagenoperna* cf. *planata* (Broili, 1903), *Pteria* aff. *seisiana* (Broili, 1903)
415 and *Badiotella* sp., which were mostly epibyssate suspension-feeders that needed a hard substratum
416 for attachment. Furthermore, gastropods from the family Patellidae were reported from the
417 Pachycardientuffe (Blaschke 1905), which also live on hard substratum.

418 Fig. 13 provides a summary of our interpretation of the fauna from the Pachycardientuffe,
419 showing transportation from the following three sources: (1) the soft ground lagoonal fauna of the
420 Schlernplateu beds, (2) the hard ground reef fauna from the Schlerndolomite and (3) a *Pachycardia*
421 *rugosa* dominated fauna from the coast from a near volcanic island.

As mentioned above, the number of species found in this study (59 species) is much lower than the number of species described by Broili (1903), Blaschke (1905), Waagen (1903) and Waagen (1907; altogether more than 270 species). One explanation for the high number of species described in these monographs is taxonomic oversplitting. A taxonomic revision of the fauna is beyond the scope of this study, but an inspection of Broili's (1903) type material in Munich confirms that his taxonomic approach was more typological than usually applied today, and that e.g. the species richness of the limid bivalve genus *Mysidioptera* (24 reported species) has been clearly overestimated. However, also the number of reported genera is higher in the literature than in our samples (100 versus 38 genera), thus oversplitting of species is not the sole reason for the difference in reported diversity. An additional factor that contributed to the higher species richness in the historical monographs is probably that these were based on a higher number of geographically distant sampling localities, which likely had different source areas and thus differed considerably in their taxonomic composition. Therefore, the lower species richness in our samples might by largely due to the poorer present-day outcrop conditions, which limited our field collections to two nearby localities.

6. Summarized interpretation of the benthic faunas from the Schlernplateau beds and Pachycardientuffe

Our field study led to the recognition of 52 species in the Schlernplateau beds and 59 species in the Pachycardientuffe. The sedimentological and palaeontological analyses outlined above allow the detailed palaeoecological interpretation of these faunas.

The recorded species from the Schlernplateau beds lived in a lagoon, close to an oceanic inlet. The fauna is unaffected from mixing by transportation, but it was probably subject to some time-

446 averaging. This means that some of the recorded species did not live contemporaneously at the same
447 place, thus the overall number of species is a certain overestimation of the community species
448 richness at a given time. However, the overall diversity of the Schlernplateau fauna represents a
449 good estimation of the taxonomic richness of shelly soft-bottom dwellers in a shallow-water setting
450 of a tropical sea at the end of the Middle Triassic.

451 In contrast to the Schlernplateau beds, the fauna of the Pachycardientuffe represents almost
452 certainly palaeocommunities from at least three different settings (lagoon, reef and sandy shallow
453 sea) that were mixed during transportation into the basin. The fact that our collection contains
454 significantly less species (59) than recorded in the literature (>270) is largely due to the lower
455 number of sampled localities that encompass a lower number of ecologically different source areas.

456 The evidence for faunal mixing in the Pachycardientuffe does not invalidate the data for studies of
457 biodiversity during the Middle Triassic, but it poses some constraints on their interpretation. The
458 fauna of the Pachycardientuffe does not represent a single palaeocommunity, but an integral of the
459 shallow marine shelly fauna that lived in different habitats at the same time. It is thus a good
460 estimator for the gamma-diversity of the reef-to-basin landscape of the tropical Tethyan ocean
461 during the late Middle Triassic.

462

463 **7. Species richness of Early and Middle Triassic benthic faunas: a comparison**

464

465 To what extend do Early and Middle Triassic benthic communities differ in their ecology, species
466 richness and taxonomic composition? Answering this question is crucial for identifying evolutionary
467 processes during the main phase of rediversification after the end-Permian mass extinction. We here
468 present a preliminary comparison between selected benthic communities of these two epochs. Data
469 used for this comparison are shown in Tab. 1. Lower and Middle Triassic macroinvertebrate faunas

selected for the comparison come from lithological units that represent similar shallow-marine environments. Because most of the data used for this comparison are raw data from the literature, synonyms and taxonomic oversplitting (see also chapter 5.2) may cause a certain bias towards greater richness, especially in Middle Triassic faunas where modern revisions mostly lack. A reevaluation of bivalve species from the Jena Fm. and the Meissner Fm. (Hautmann, unpublished data) suggests oversplitting by nearly 50%. However, because oversplitting is likely similar in all major taxa, the gastropod/bivalve ratio discussed below is probably robust, and a pronounced Anisian rise in diversity maintains even if an overestimation of diversity by factor 2 is assumed.

The comparison between Early and Middle Triassic benthic communities shows clearly that the overall diversity increased through time; however, diversity slowly increased during the Early Triassic and rapidly during the Middle Triassic (Tab. 1; Fig. 14a). This pattern is evident in the trends of the most diverse taxa in Early and Middle Triassic benthic communities, i.e., bivalves, gastropods and brachiopods. Our compilation shows that bivalves were clearly the most diverse taxon in Early Triassic benthic communities. Although bivalves were relatively diverse immediately after the end-Permian mass extinction, the net increase in species richness was small until the end of the Early Triassic. The major diversification of bivalves occurred during the Anisian (Hautmann 2007; Tu et al. 2016). Already the Late Bithynian–Early Illyrian Jena Fm. yields a highly diverse Middle Triassic bivalve fauna, surpassed by the late Anisian fauna of the Leidapo Mb. (Tab. 1). Gastropods were on average the second most diverse taxon during the Early Triassic, and their increase in species richness during that time was comparable to that of bivalves. During the Middle Triassic, however, gastropod species richness increased more rapidly than bivalve species richness. In consequence, gastropods were the most diverse group in many Middle Triassic lithological units (Tab. 1). The change from the taxonomic dominance of bivalves in Early Triassic benthic communities to the taxonomic dominance of gastropods during the Middle Triassic can also be seen in the gastropod/bivalve-ratio that was variable but with an increasing trend through time (Fig. 14b). Brachiopods were the third most diverse group in almost all Early and Middle Triassic benthic

communities. Their species richness was relatively low during the Early Triassic, and in most Olenekian lithological units used for this comparison they are even not reported. However, brachiopods also became more diverse during the Middle Triassic, although their increase in species richness during the Middle Triassic is much slower compared to bivalves and gastropods.

The comparison between Early and Middle Triassic benthic communities confirms that corals were absent in the entire Early Triassic (e.g., Flügel 2002; Weidlich et al. 2003; Stanley 2003; Payne et al. 2006; Brayard et al. 2011). Sponges occurred only in two Lower Triassic formations used for this comparison, but sponges, in association with microbialites, are known from the Lower Triassic (Induan) of Armenia (Friesenbichler et al. 2018), Lower and Middle Triassic carbonate successions of the Western Tethys domain (the Alps, Carpathians and the Germanic Basin; ~~Sculz~~Szulc 2007) as well as Lower Triassic strata from China (Ezaki et al. 2008; Bagherpour et al. 2017) and the Western US (Brayard et al. 2011; Hofmann et al. 2014). However, the number of these sponge species is not known. Middle Triassic sponges are not only reported in the lithological units shown in Tab. 1 but also in the Illyrian strata of the Wetterstein Fm. (Velledits et al. 2011). The fossil record of echinoderms in the Early to Middle Triassic is heterogeneous. Several Palaeozoic clades of echinoderms survived the end-Permian mass extinction and reappeared as Lazarus taxa in the Middle Triassic, without giving rise to a new diversification (Thuy et al. 2017). Crinoid diversity was very low during the Early Triassic (Hagdorn 2011), although cladistics analyses suggest that initial diversification took place in the Induan (Twitchett and Oji 2005) or already in the Late Permian (Oji and Twitchett (2015); however, well before the documented species richness increase during the Middle and early Late Triassic (Hagdorn 2011). Only two echinoid genera are reported from Lower Triassic strata (Twitchett and Oji 2005) and very low levels of diversity were apparently maintained for at least the duration of the Early and Middle Triassic. Nevertheless, numerous undescribed echinoid spines and other remains have been noted in Early Triassic fossil assemblages (e.g., from the Griesbachian of Oman; Krystyn et al. 2003) and these undescribed records may hint at a hidden diversity of echinoids within the Early Triassic (see also Thompson et al. 2015; Thuy et al. 2017). Fossil

522 remains or trace fossils attributed to Lower Triassic asteroids have only been recorded from
523 Olenekian strata of the western USA (Schubert and Bottjer 1995; Villier et al. 2018). Definite reports
524 from Lower Triassic holothuroids only exist from Western Nepal (Kozur and Mostler 1973; Mostler
525 1977), whereas a total number of 84 holothuroid species was reported from several Middle Triassic
526 strata (Reich 2013). Fossil remains from ophiuroids are quite abundant in Lower Triassic strata
527 worldwide but so far only six species have been described (Twitchett and Oji 2005). Early Triassic
528 bryozoans were reported from a couple of Lower Triassic strata (Nakrem and Mørk 1991; Wignall and
529 Twitchett 2002; Baud et al. 2008) but only five Early Triassic bryozoan genera are reported (Powers
530 and Pachut 2007) and only six species have been described formally (Baud et al. 2008); however,
531 bryozoan diversity increased during the Middle and Late Triassic, with eight reported genera (Powers
532 and Pachut 2007) a total number of more than 40 species (see reviews in Schäfer and Grant-Mackie
533 1994; Schäfer et al. 2003). Microconchids were important constituents of marine ecosystems
534 immediately after the Permian/Triassic mass extinction (He et al. 2012) and were also commonly
535 present through the entire Early Triassic worldwide (Fraiser 2011; Zatoń et al. 2013b; Yang et al.
536 2015). Although microconchids can be very abundant locally, they are lowly diverse and only
537 represented by three genera (Zatoń et al. 2013b).

538 The Middle Triassic increase in species richness might be related to more stable environmental
539 conditions, as reflected by the constancy of the Middle Triassic carbon isotope curve (Payne et al.
540 2004), or alternatively represent the effect of competition-driven niche partitioning after
541 rediversification exceeded a threshold (Hautmann 2014; Hautmann et al. 2015). The change in the
542 gastropod/bivalve-ratio is more difficult to interpret, but it is notable that occurrences of high
543 gastropod species richness relative to bivalves are almost exclusively linked to carbonate platform
544 environments (Fig. 14b). This might represent a taphonomic bias due to differences in skeletal
545 mineralogy between gastropods and bivalves, but we note that aragonite-shelled bivalves are
546 commonly preserved in the Early Triassic, which makes this explanation unlikely. Alternatively, we
547 hypothesise that the increase in gastropod species richness is a primary signal linked to the

548 resurgence of large carbonate platform and reefs during the Middle Triassic (Gaetani et al. 1981;
549 Senowbari et al. 1993), although details of the ecological causes for this facies-related increase in
550 gastropod species richness requires further investigation.

551

552 **8. Conclusion**

553

554 Early and Middle Triassic shallow-marine benthic communities differed considerably in terms of
555 species richness and taxonomic composition. Whereas Early Triassic formations from shallow-marine
556 settings contain generally less than 50 macroinvertebrate species, regional diversities of around 300
557 species have been described from various Anisian-Ladinian shallow-marine settings worldwide (Tab.
558 1; Fig. 14), including the herein studied fauna from the Pachycardientuffe. For more narrowly defined
559 habitats, such as that of the open lagoon represented by the Schlernplateau fauna (85 species), the
560 increase in diversity was likewise remarkable. The Middle Triassic increase in diversity at the
561 local/regional level analysed herein correlates with the most pronounced increase in bivalve diversity
562 during the entire Triassic in a global dataset (Hautmann 2007, fig. 8) and therefore represents the
563 main phase of recovery after the end-Permian mass extinction. This main phase of recovery in
564 benthic marine communities was associated with a weakening of the dominance of bivalves in
565 comparison to the Early Triassic, which reflects the proliferation of other invertebrate taxa,
566 particularly gastropods. We hypothesise that the resurgence of carbonate platforms during the
567 Middle Triassic played an important role in the shift of taxonomic compositions, and that the
568 increase of environmental diversity associated with newly arising carbonate platforms contributed at
569 least partly to the accelerated pace of recovery during the Middle Triassic.

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Figure captions

Fig. 1 Locality map showing the position of the studied sections at the Seiser Alm/Alpe di Siusi (red stars) and the Schlern/Sciliar (blue stars). GPS-coordinates are N 46°30'40.8'', E 11°33'48.54'' for Schlern locality A and N 46°30'36.19'', E 11°33'51.9'' for Schlern locality B

Fig. 2 Field photographs. (a) Sampling locality Frommerbach A, showing the investigated section (see also Fig. 10 [left]). Scale = 1 m. (b) Sampling locality Frommerbach B, showing the investigated section (see also Fig. 10 [right]). (c) Western flank of the Seiser Klamm/Gola di Siusi showing the Schlernplateau beds (SchPl. beds), the post-volcanic bedded facies of the Rosszähne Fm. (RZ), volcanic rocks (V) and the pre-volcanic Schlerndolomite of the Rosengarten Fm. (R). The white rectangle indicates the position of (d). (d) Detailed look on the Schlernplateau beds. (e) Bioclastic rudstone from top of the Schlernplateau beds containing gastropods and bivalves. (f) Oncolites from the western Schlernplateau. Coin (16 mm) for scale

Fig. 3 Section of the Schlernplateau beds from the western flank of the Seiser Klamm/Gola di Siusi. M = marl, m = mudstone, w = wackestone, p = packstone, g = grainstone, SP = Schlernplateau. The Ladinian/Carnian boundary lies within bed SP10

Fig. 4 Rarefaction analyses from the Schlernplateau beds (a) and the Pachycardientuffe (b). Only samples with more than 40 individuals were analysed. See text for details. SP = Schlernplateau, SK = Seiser Klamm, SK-E = end of Seiser Klamm, FB = Frommmerbach

Fig. 5 Most common bivalves and gastropods collected at the Schlernplateau. (1) *Trigonodus costatus* von Wöhrmann and Koken, 1892, left valve interior (1A) and left valve exterior (1B), PZO5984, bed SP7. (2) *Cassianella bipartita* (von Klipstein, 1845), left valve, PZO5988, bed SP8. (3) *Entolioides zitteli* (von Wöhrmann and Koken, 1892), right valve, PZO5986. (4) *Myophoriopis richthofeni* (Stur, 1868), left valve, PZO5985, bed SP10. (5) *Myophoria kefersteini* (Münster in Goldfuss, 1837), left valve, PZO5987, bed SP8. (6) '*Loxonema*' *lineatum* von Wöhrmann and Koken, 1892, PZO5994, bed SP8. (7) '*Loxonema*' *aequale* von Wöhrmann and Koken, 1892, PZO5990, bed SP7. (8) *Stephanocosmia coronata* (von Wöhrmann and Koken, 1892), PZO5989. (9) *Zygopleura spinosa* von Wöhrmann and Koken, 1892, PZO5995bed SP8. (10) *Pustularia alpina* von Eichwald, 1851, PZO5998. (11) *Tretospira multistriata* von Wöhrmann and Koken, 1892, PZO5997, bed SP8. (12) *Coelostylina solida* (von Wöhrmann and Koken, 1892), PZO5996, bed SP7. (13) *Neritaria plicatilis* (von Klipstein, 1844), PZO5993, bed SP8. (14) *Naticopsis neritacea* (Münster, 1841), PZO5991, bed SP7. (15) *Palaeonarica concentrica* (Münster, 1841), PZO5992, bed SP7. Scale bars represent 1 cm for bivalves and 0.5 cm for gastropods

Fig. 6 Bivalves from the Pachycardientuffe. (1) *Pachycardia rugosa* von Hauer, 1857, right valve exterior (1A) and right valve interior (1B), PZO5980, bed FB B1. (2) *Heminajas fissidentata* (von Wöhrmann, 1889), left valve, PZO5983, bed FB A3. (3) *Pteria kokeni* (von Wöhrmann and Koken, 1892), left valve, PZO5982. (4) *Pachycardia plieningeri* Broili, 1903, left valve interior (4A) and left valve exterior (4B), PZO5981, bed FB B1. (5) *Myoconcha parvula* von Wöhrmann and Koken, 1892, right valve, SMNHS75537. (6) *Pteria salomoni* (Broili, 1903), right valve, SMNHS75534/1-2. (7) *Myoconcha curvata* Broili, 1903, left valve interior and left valve exterior, SMNHS10274. (8) *Mysidioptera interrupta* Broili, 1903, left valve, SMNHS17501/162. (9) *Trigonodus rablensis* (Gredler, 1862), right valve exterior (9A) and left valve interior (9B), 10284/1-3. (10) *Waagenoperna planata* (Broili, 1903), left valve, SMNHS17501/45. (11) *Mysidioptera emiliae* Bittner, 1900, right valve, SMNHS17501/12. (12) *Pteria tofanae* (Bittner, 1895), left valve, SMNHS75538, collected at

1008 Tschapitbach. (13) *Newaagia lata* (von Klipstein, 1845), right valve interior, SMNHS75536. (14)
1009 *Parallelodon tschapitana* (Broili, 1903), right valve, SMNHS17501/250. Scale bars represent 1 cm

1010

1011 **Fig. 7** Q-mode (samples) and R-mode (species) cluster analysis of samples with more than 40
1012 individuals from the Schlernplateau beds using unweighted pair-group average and Morisita
1013 similarity index. The circle sizes represent the abundance of species within the corresponding sample
1014 (small circle = 1 individual, small medium-sized circle = 2-5 individuals, big medium-sized circle = 6-20
1015 individuals, big circle = more than 20 individuals). SP = Schlernplateau, SK = Seiser Klamm, SK-E = end
1016 of Seiser Klamm. See text for details

1017

1018 **Fig. 8** Rank-abundance distributions and guild-structures of the entire fauna of the Schlernplateau
1019 beds (a) and Pachycardientuffe (b). n = total number of individuals

1020

1021 **Fig. 9** Rank-abundance distributions and guild-structures of representative fossiliferous beds SP14
1022 (a), SP7 (b) and SP3 (c) from the Schlernplateau beds (see also Fig. 3). n = total number of individuals

1023

1024 **Fig. 10** Sections Frommerbach A and B of the Pachycardientuffe from the Seiser Alm/Alpe di Siusi

1025

1026 **Fig. 11** Rank-abundance distributions and guild-structures from the fossiliferous beds FB A3 (a), FB B2
1027 (b) and FB B1 (c) from the Pachycardientuffe (see also Fig. 10). n = total number of individuals

1028

Fig. 12 Lithological samples from locality Frommerbach A showing the highly fossiliferous limestone (a) and volcanoclastic sandy siltstone (b-c) containing disarticulated, randomly arranged bivalves. Scales are 23 mm (diameter of the coin) for (a) and 5 cm for (b) and (c)

Fig. 13 (a) Palaeoenvironmental reconstruction of the Schlern and Seiser Alm area during the Late Ladinian showing the distribution of sedimentary facies and the potential source areas of the Pachycardientuffe. (b) Panorama image taken from the top of the eastern margin of the Schlern mountain, showing present-day position of the former lagoon (Schlernplateau beds, 1), the post-volcanic reef (Rosszähne Fm., 2), the probable position of the suggested volcanic island (3) and the basin (Seiser Alm basin, Pachycardientuffe and Wengen Fm., 4)

Fig. 14 Diversity changes throughout the Early and Middle Triassic based on data shown in Tab. 1; see text for further explanation. (a) Total number of species. (b) Gastropod/bivalve-ratio. Blue lines mark formations with carbonate platform facies. G = Griesbachian; D = Dienerian; Sm = Smithian; Sp = Spathian, A = Aegean; B = Bithynian; P = Pelsonian; I = Illyrian; F = Fassanian; L = Longobardian; J = Julian; Carn. = Carnian; LT = Late Triassic. Marmolada = Marmolada Limestone; PachyT = Pachycardientuffe; Latemar = Latemar Limestone; SchPl = Schlernplateau beds

Table captions

Tab. 1 Benthic species richness of selected Early and Middle Triassic faunas. B = bivalves, G = gastropods, Br = brachiopods, C = corals, Sp = sponges, Cr = crinoids, E = echinoids, A = asteroids, Bry = bryozoans, Cru = crustaceans, H = holothurioids, M = microconchids, O = ophioroids, Pc = polychaete worms, Pp = polyplacophorans, Sc = scaphopods, ? = these taxa were reported but the exact number of species is unknown. Information about the age of the lithological units come from Fürsich and Wendt 1977, Broglio Loriga et al. 1990, Brack and Rieber 1993, Brack et al. 1996, Vörös 2003, Manfrin et al. 2005, Stiller and Bucher 2008, Hagdorn and Nitsch 2009, Shigeta et al. 2009, Balini et al. 2010, Hofmann et al. 2013a, 2013b, 2014, 2015, Urlichs 2014, Foster et al. 2015, 2017, Hausmann and Nützel 2015, Hautmann et al. 2015, Brayard et al. 2017, Foster and Sebe 2017. See text for details

Online Resources captions

Online Resource 1 Excel tables showing the quantitative matrix of fossil occurrences used for data analyses, the comparison between the faunas of the Schlernplateau beds and the Pachycardientuffe as well as the number of species, number of individuals and Simpson-D values for each fossiliferous bed

Figure

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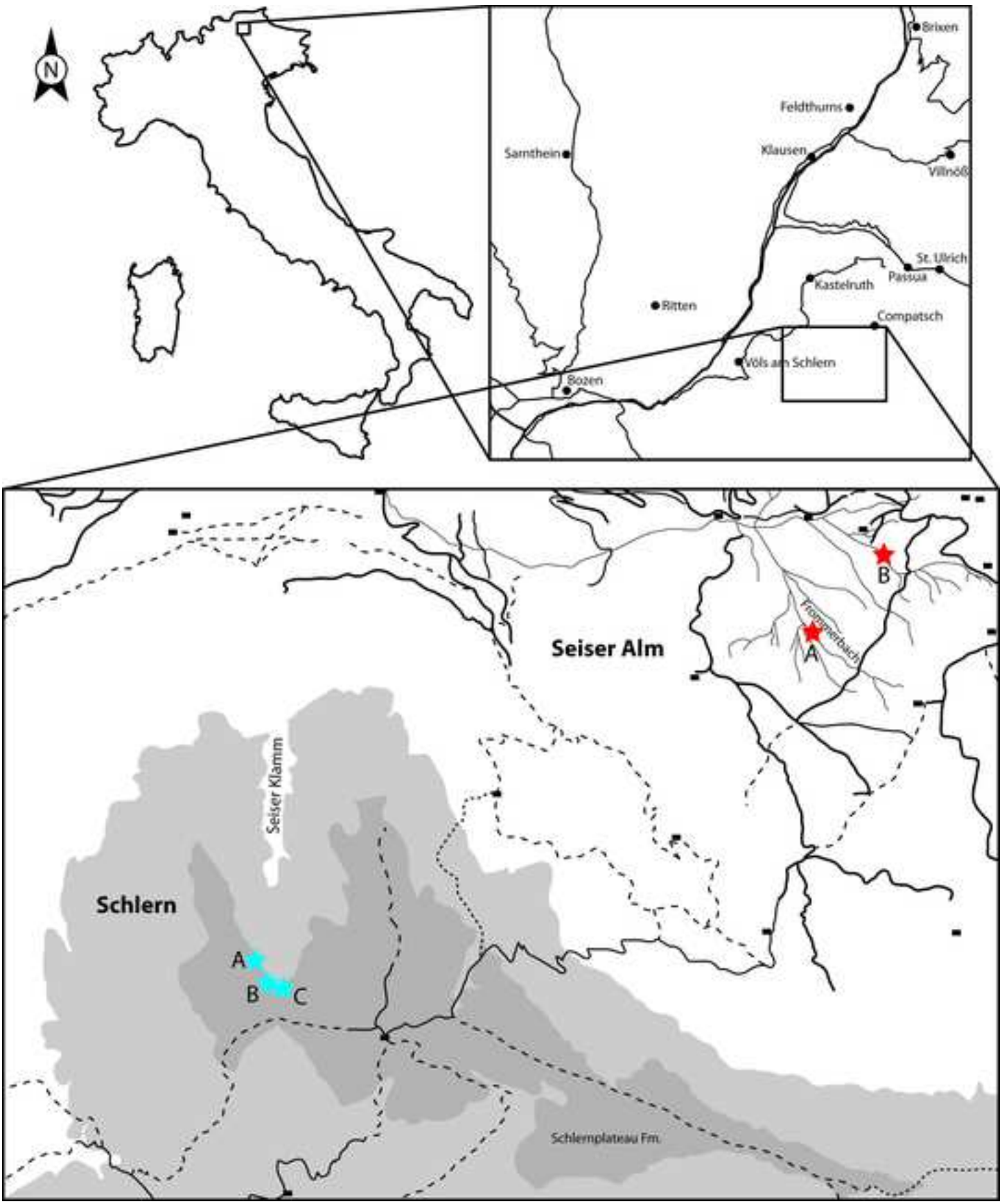

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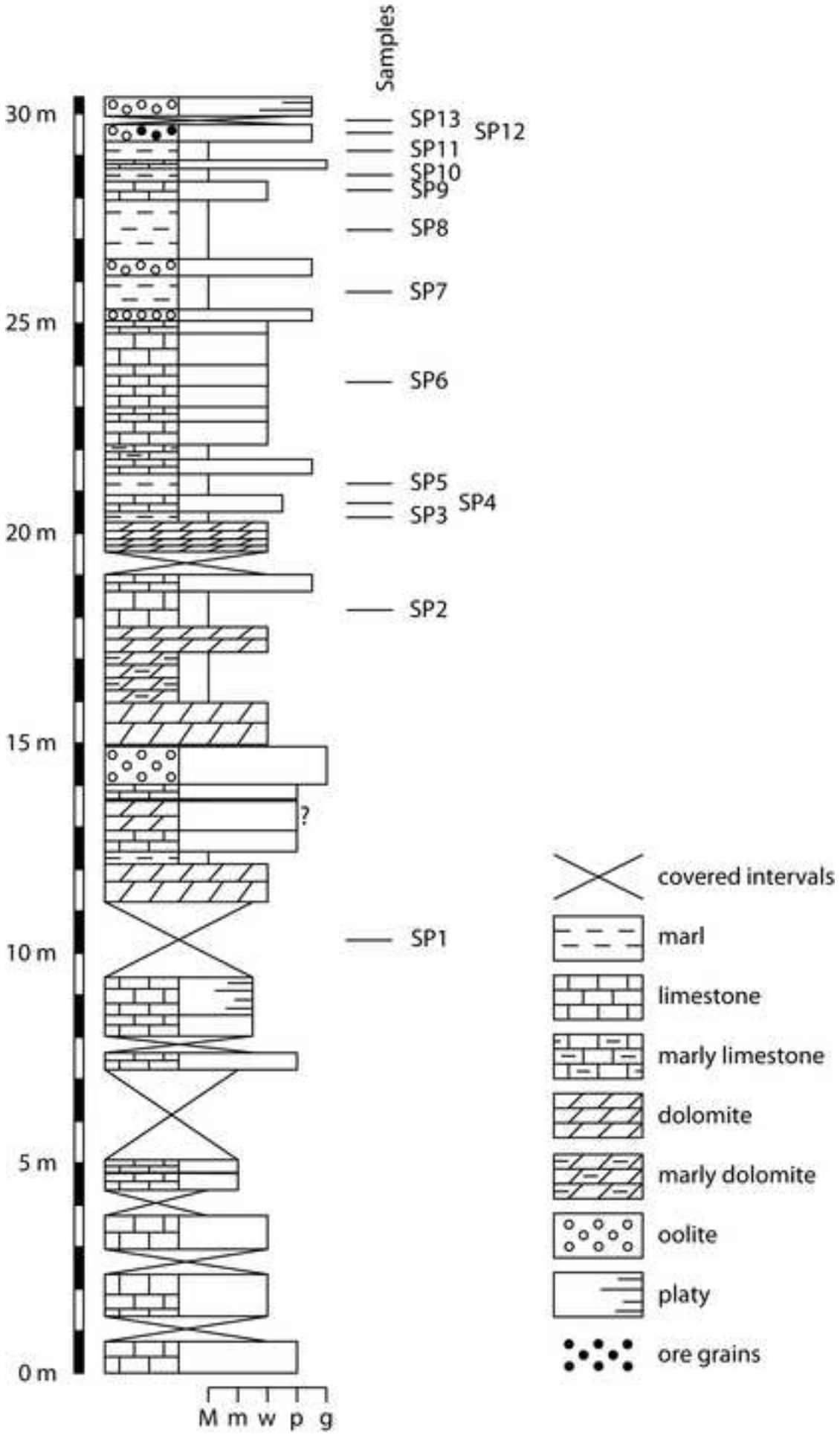

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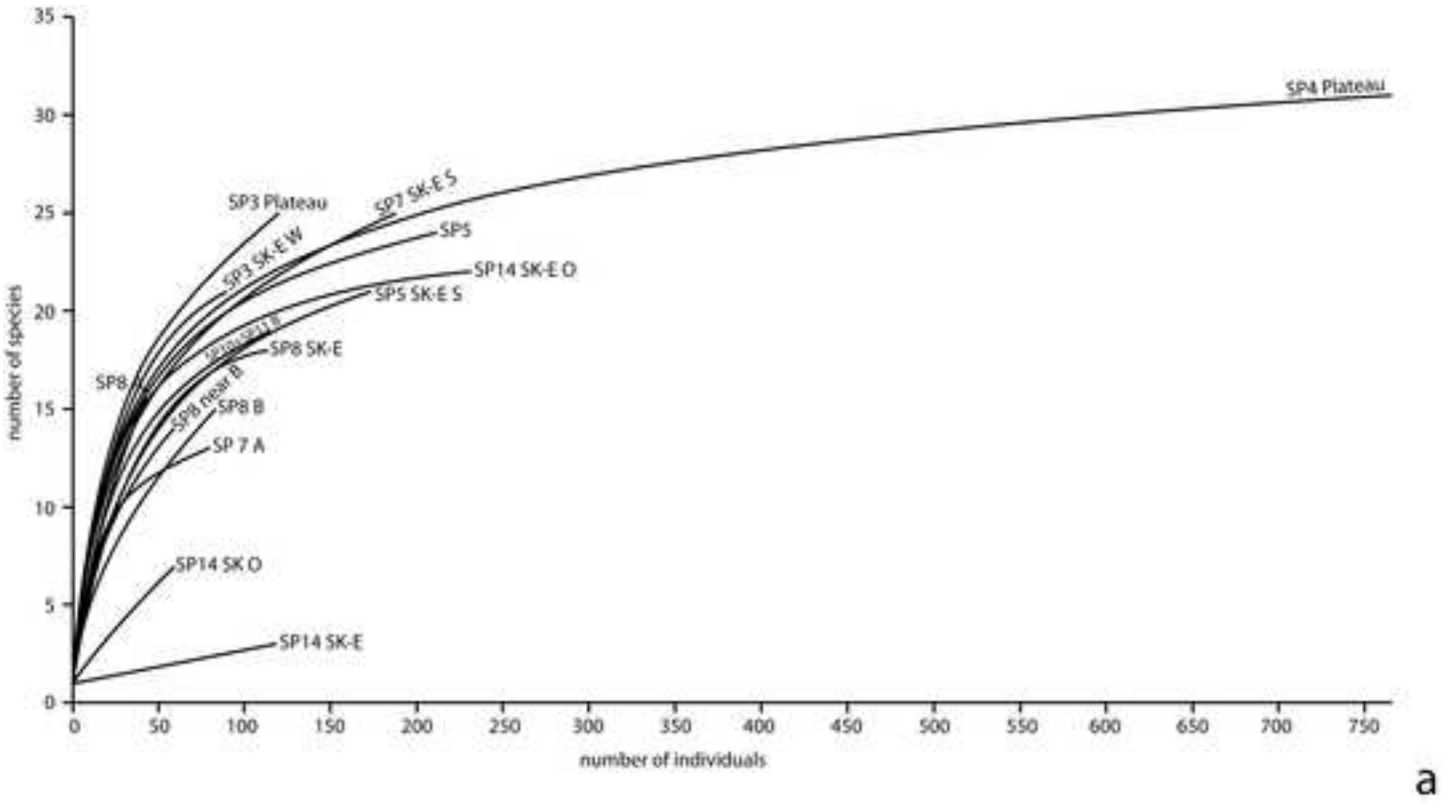

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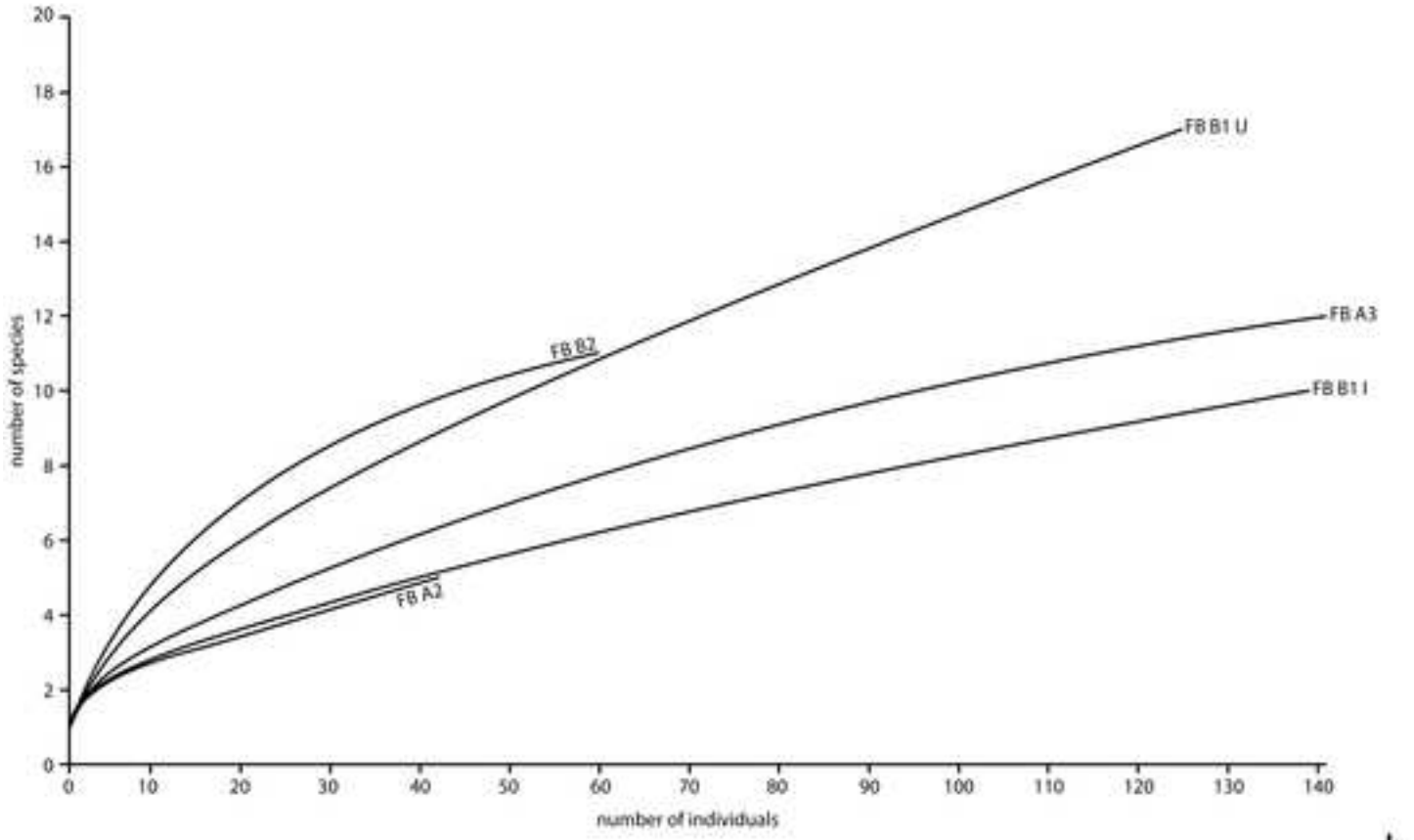

b

Figure

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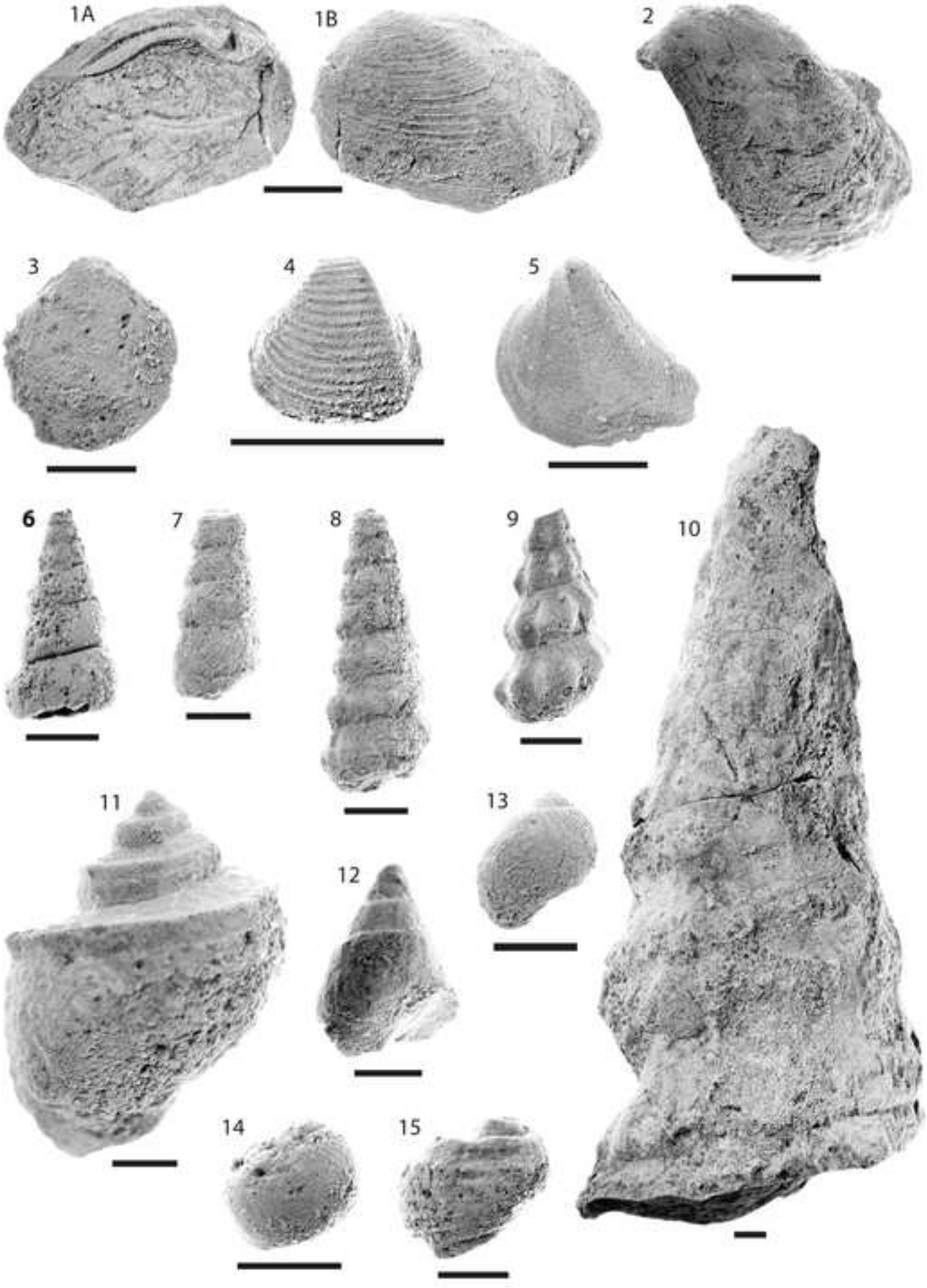

Figure

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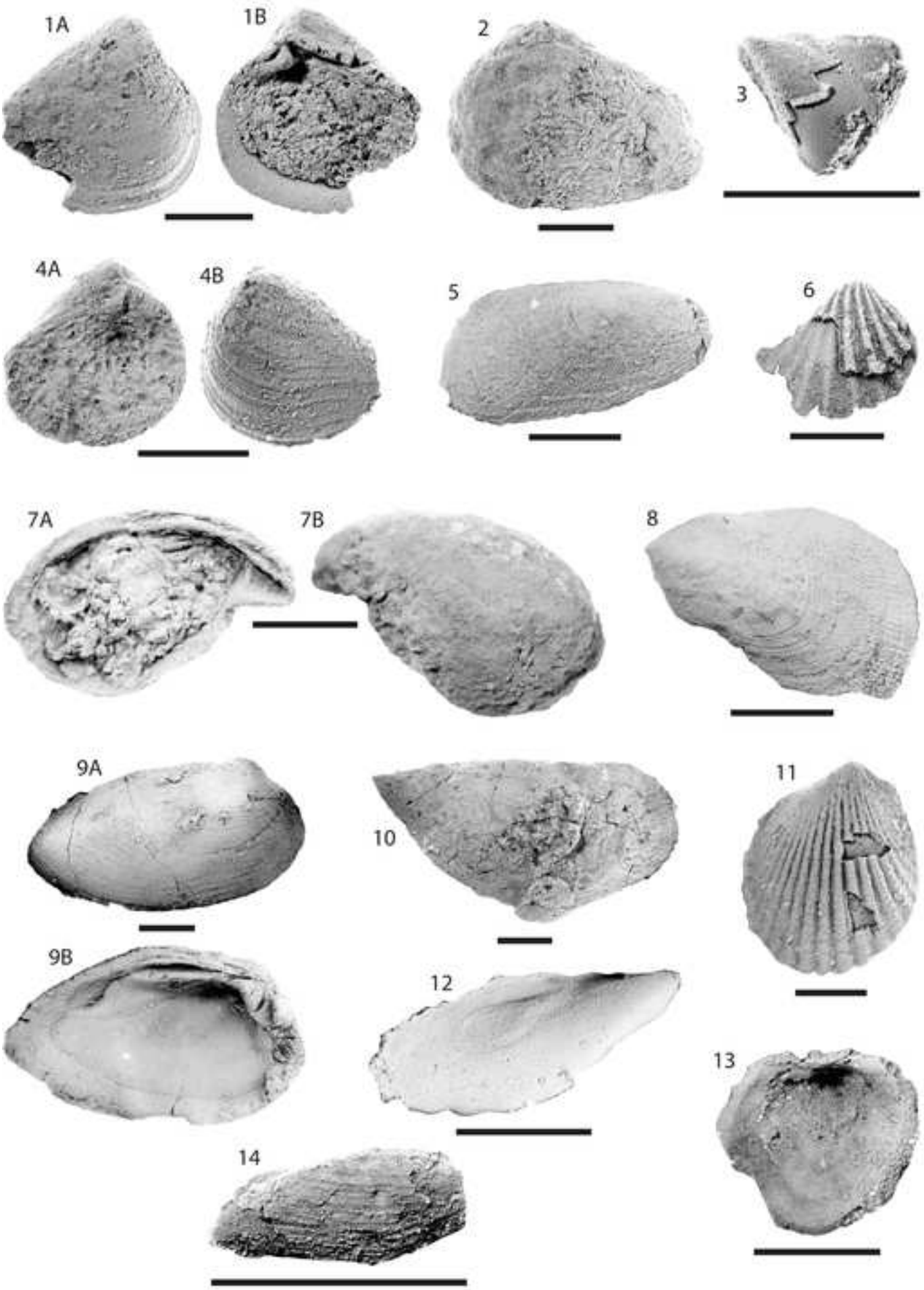

Figure

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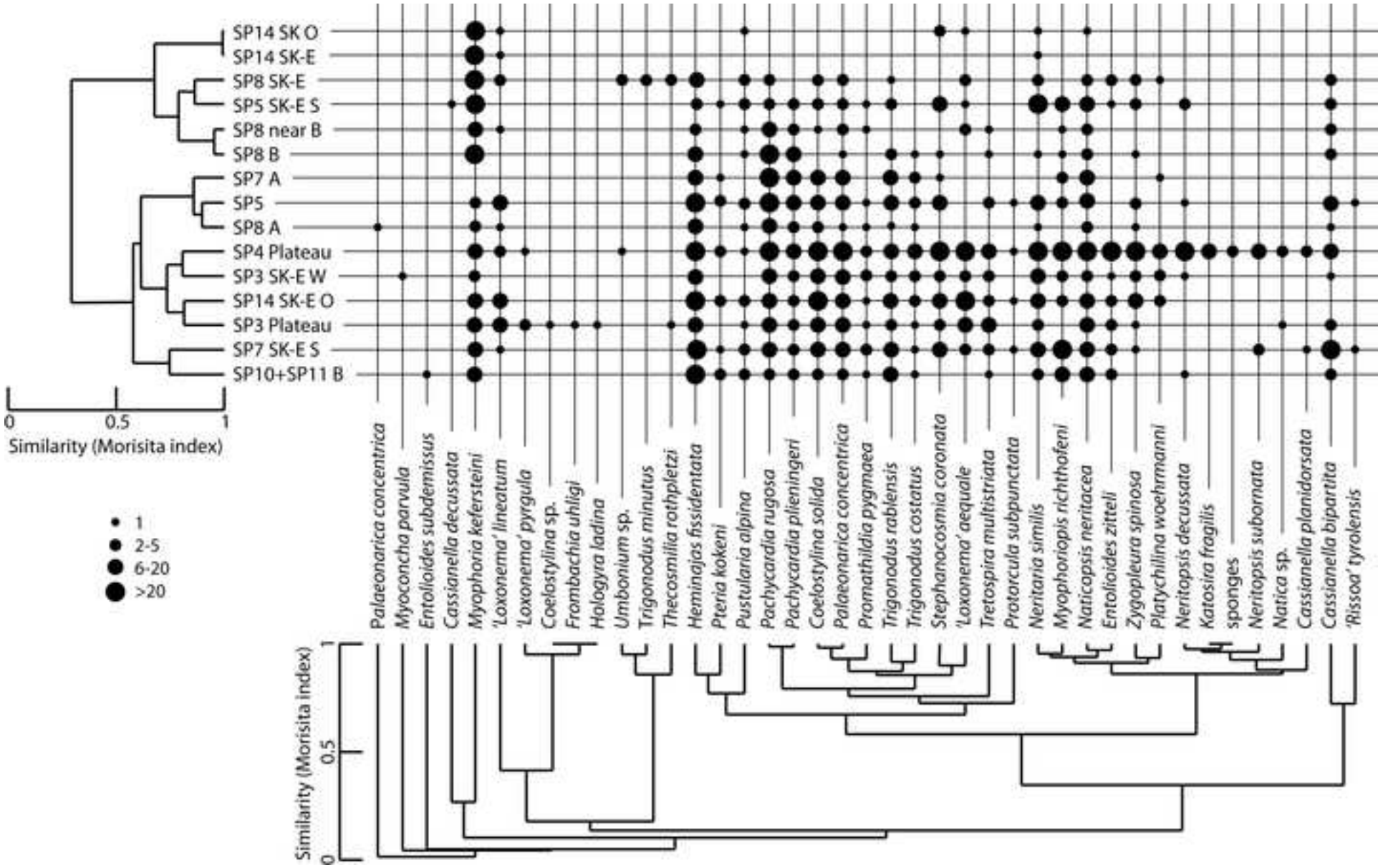

Figure

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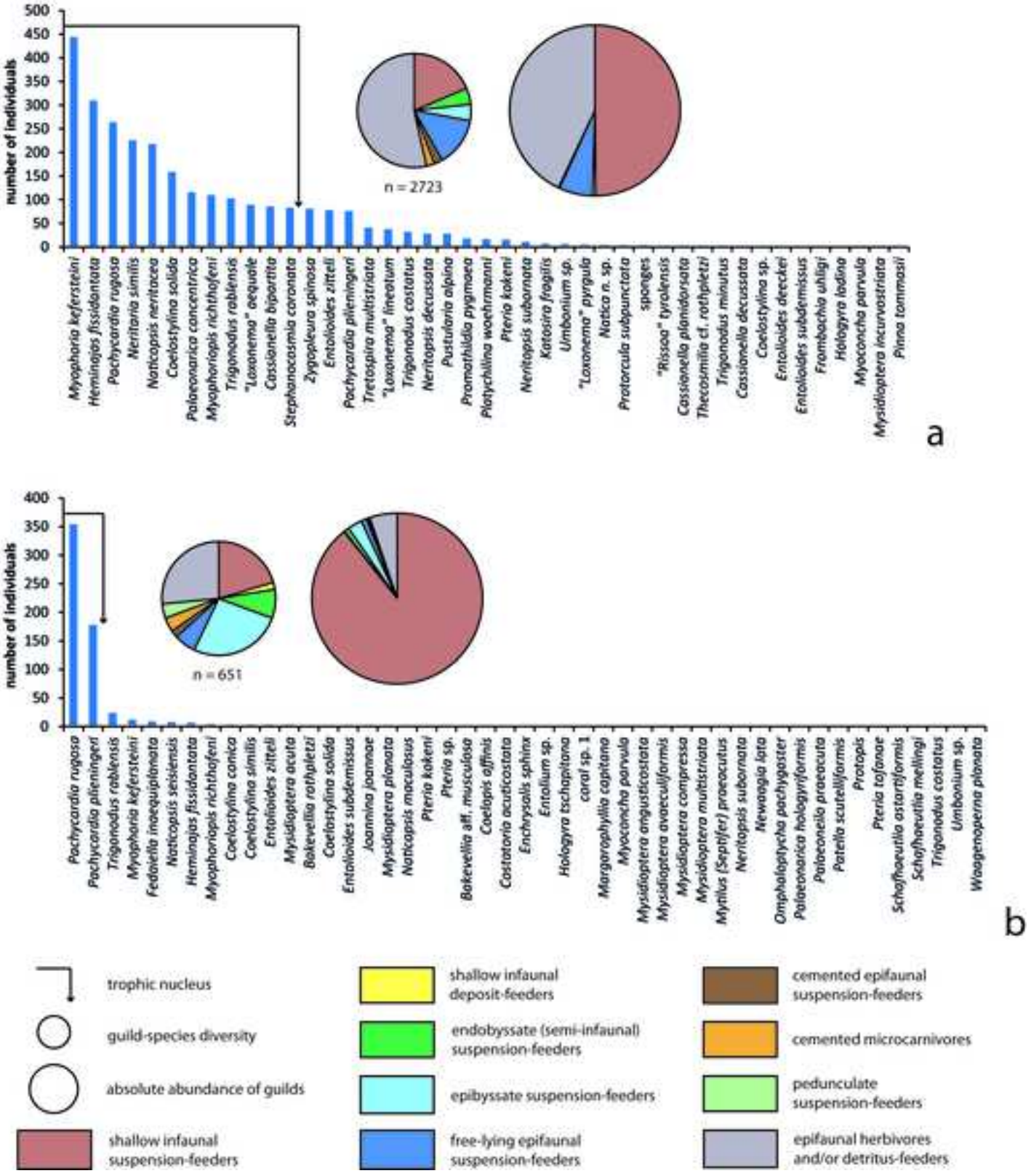

Figure

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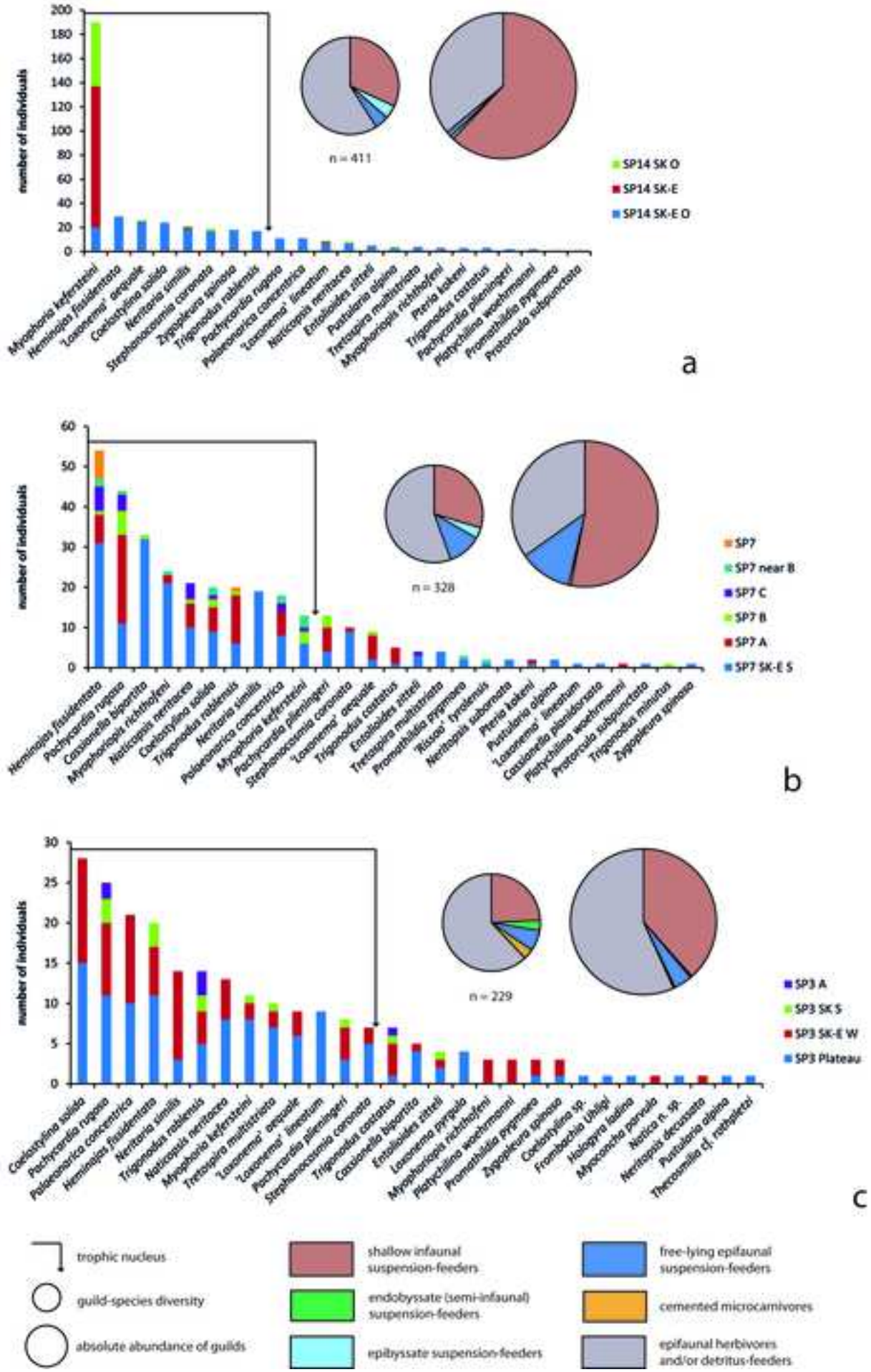

Figure

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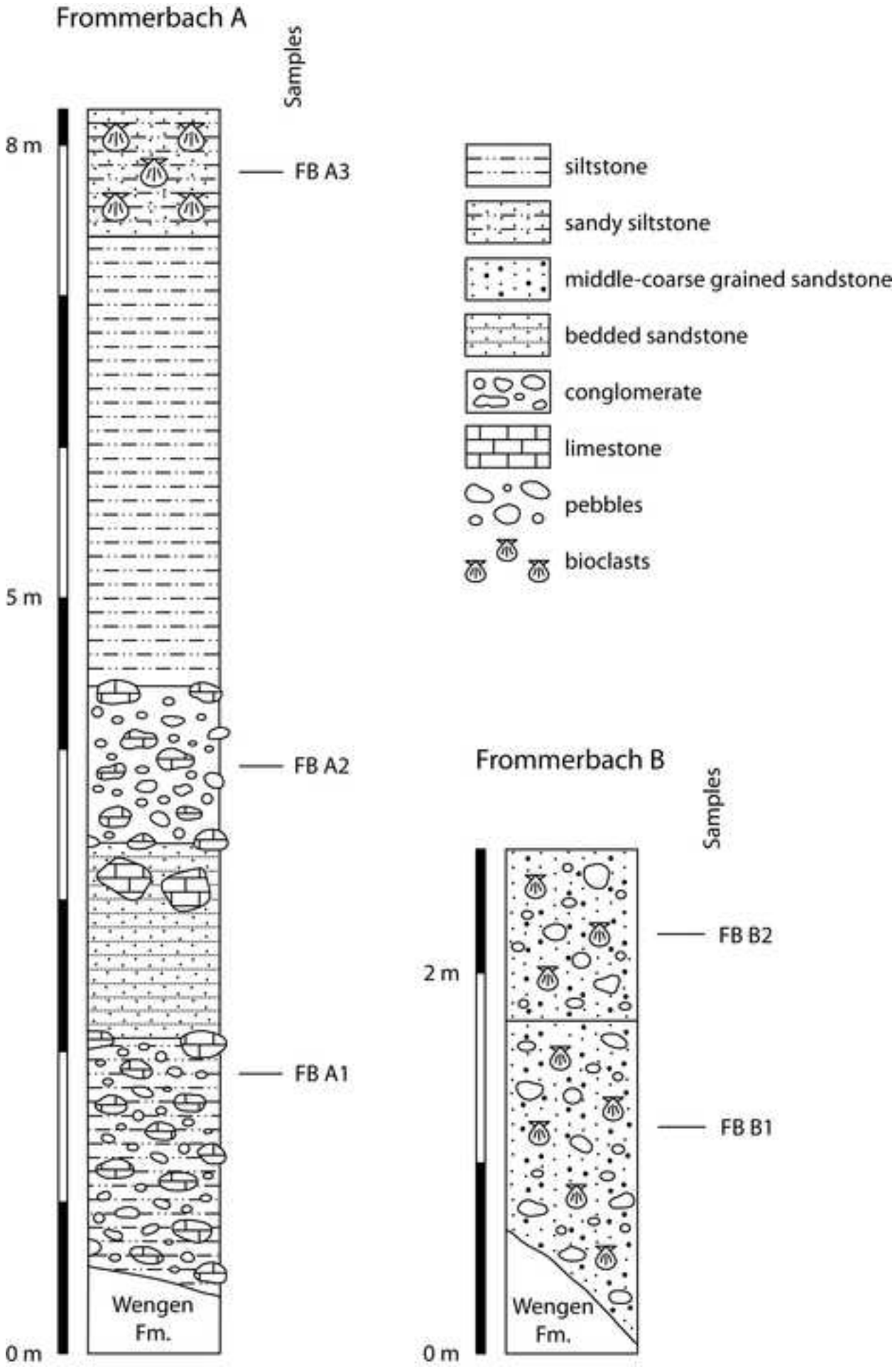

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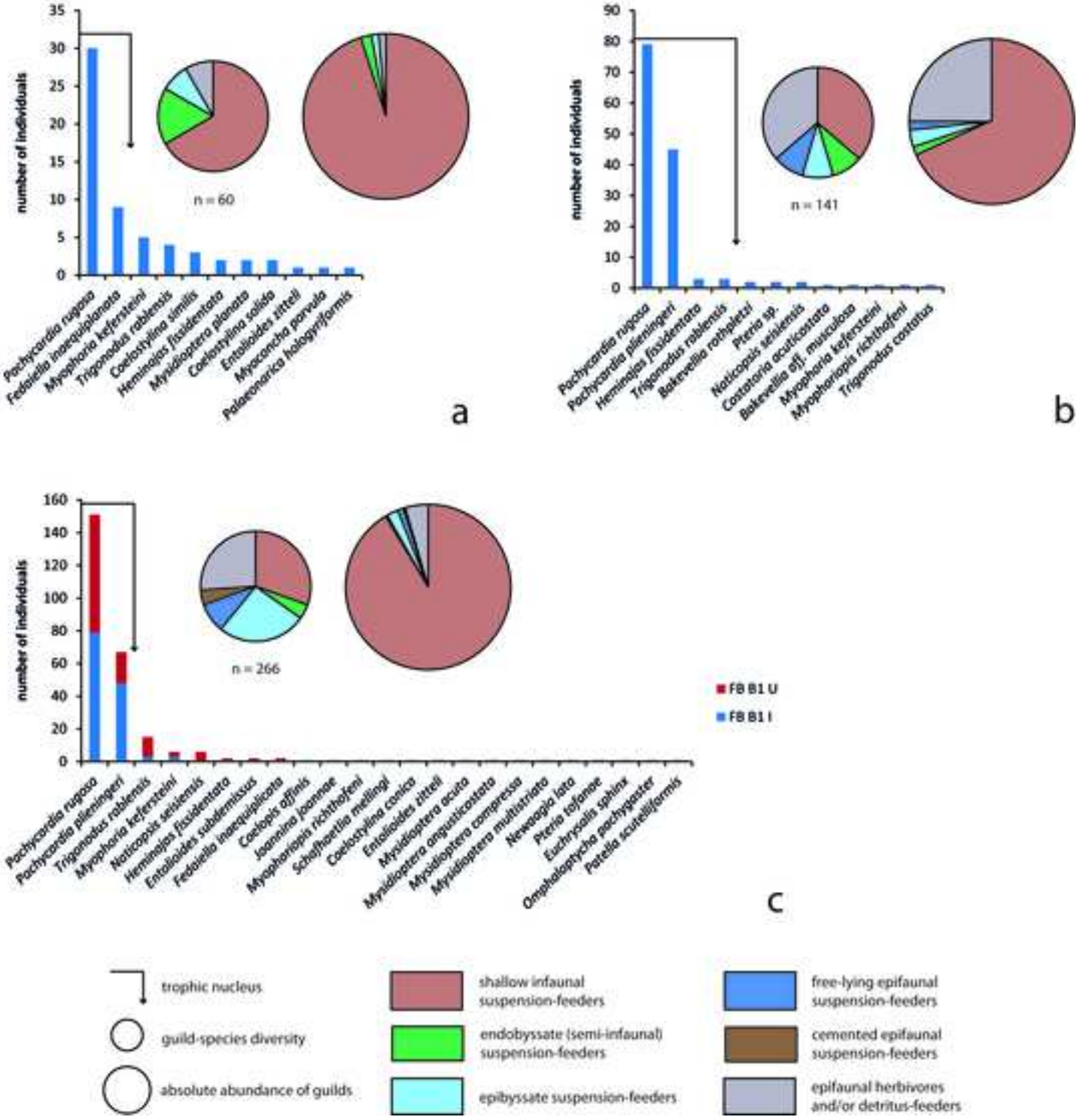

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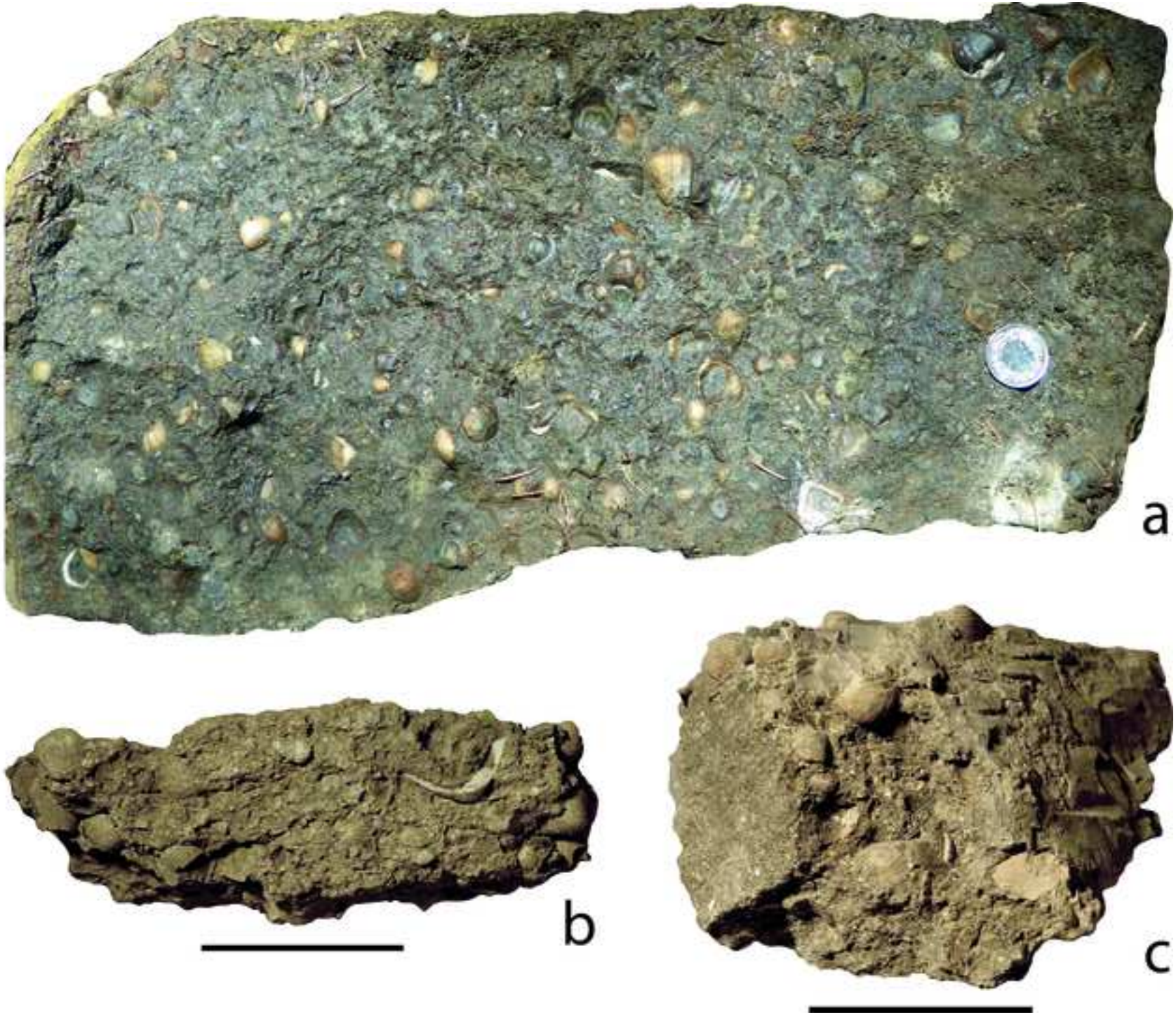

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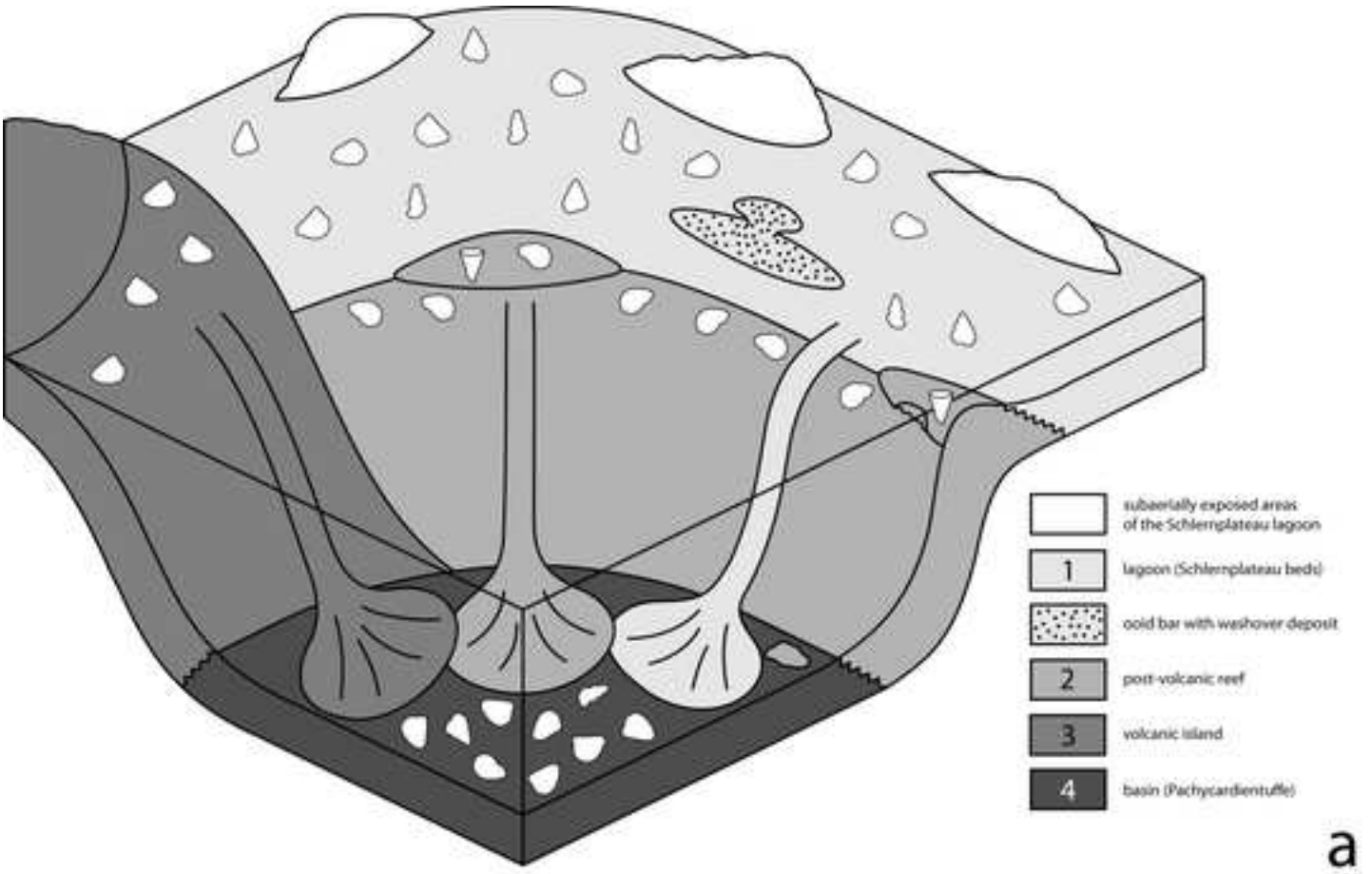

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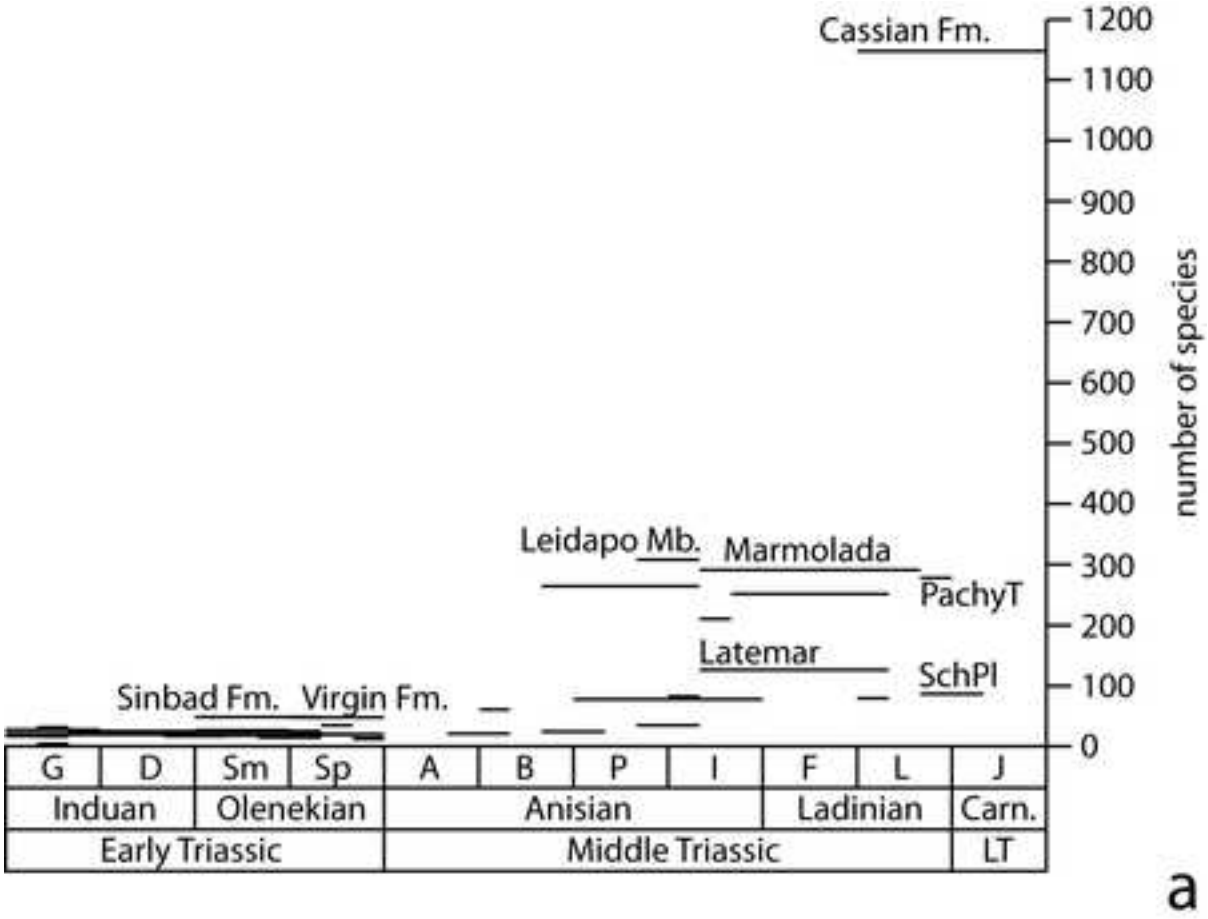

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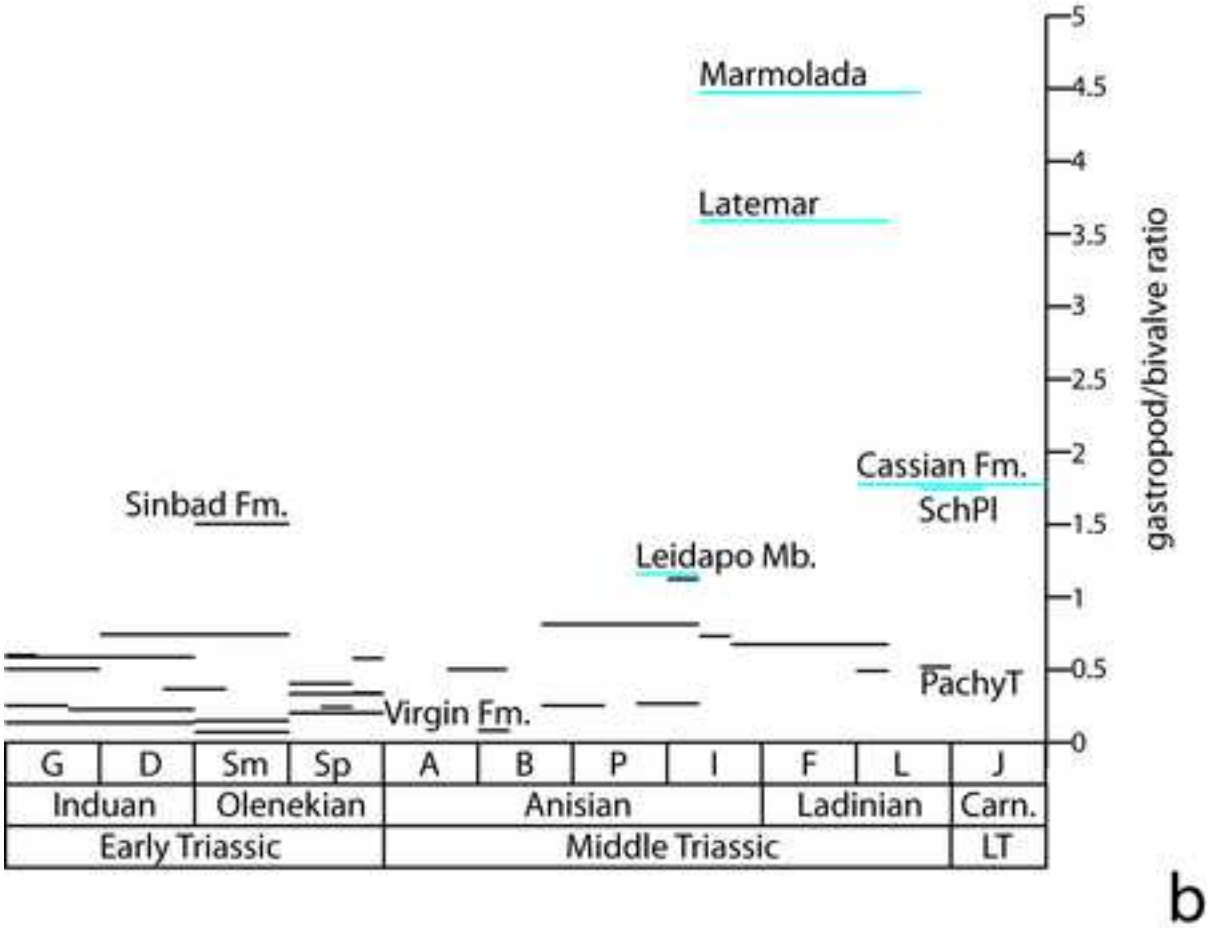

b

Table

lithological unit	age	total number of benthic species	number of species								reference(s)
			B	G	Br	C	Sp	Cr	E	others (A, Bry, Cru, H, M, O, Pc, Pp, Sc)	
Cassian Fm. (Italy)	Longobardian–Julian	1146	296	525	110	72	79	15	34	5 H 4 Sc 3 O 2 Bry 1 Pc	Laube (1865a-b, 1868, 1869a), Kittl (1891, 1892, 1894), Bittner (1890, 1892, 1895), Volz (1896), Pia (1937), Leonardi and Fiscon (1947, 1959), Frizzell and Exline (1955), Fürsich and Wendt (1977), Zardini (1978, 1981), Nützel and Kaim (2014), Hausmann and Nützel (2015)
Schlernplateau beds (Italy)	Late Longobardian–Early Julian	85	27	47		5	?	2	4		von Wöhrmann and Koken (1892), Blaschke (1905), this study
Pachycardientuffe (Wengen Fm., Italy)	Late Longobardian	277	150	77	24	5	3	4	13	1 Sc	Broili (1903), Blaschke (1905), Waagen (1903, 1907), Fürsich and Wendt (1977), this study
Erfurt Fm. ("Lower Keuper", Germany)	Early Longobardian	78	47	23	5					2 Cru 1 Pc	Schmidt (1928, 1938), Urlichs (1982)
Meissner Fm. (upper part of the „Upper Muschelkalk", Germany)	Late Illyrian–Early Longobardian	250	118	79	10	3	1	2	5	14 Cru 9 O 5 Pc 2 Sc 1 A 1 M	Wagner (1897), Schmidt (1928, 1938), Busse (1972), Hagdorn and Mundlos (1982), Hagdorn and Ockert (1993), Zatoń et al. (2013a)
Marmolada Limestone (Italy)	Middle Illyrian–Middle Longobardian	290	45	201	31	7		2	3	1 Cru	Böhm (1895), Salomon (1895)
Latemar Limestone (Italy)	Middle Illyrian–Early Longobardian	125	24	86	15						Häberle (1908), Wilckens (1909)

Trochitenkalk Fm. (basal part of the “Upper Muschelkalk”, Germany)	Middle Illyrian	209	96	70	5	2	1	2	5	10 Cru 9 O 5 Pc 2 Sc 1 A 1 M	Wagner (1897), Schmidt (1928, 1938), Busse (1972), Hagdorn and Ockert (1993), Ockert (1993), Urlichs (1992), Hautmann and Hagdorn (2013), Zatoń et al. (2013a)
Karlstadt Fm., Heilbronn Fm., Diemel Fm. („Middle Muschelkalk“, Germany)	Early Illyrian	81	34	38	3	1	?	1	1	2 Pc 1 Cru	Schmidt (1928, 1938)
Leidapo Mb. (Quingyan Fm., China)	Late Pelsonian–Early Illyrian	308	109	126	27	8	3	8	17	4 Bry 3 Sc 3 V	Yin and Yochelson (1983a-c), Stiller (2001), Komatsu et al. (2004)
Zuhánya Limestone (Hungary)	Late Pelsonian–Early Illyrian	33	19	5	2			3	1	1 M 1 O 1 Sc	Foster and Sebe (2017)
Felsőörs Fm. (Hungary)	Pelsonian–Illyrian	77	39		35			1		2 H	Szabó et al. (1979), Vörös (2003)
Jena Fm. (“Lower Muschelkalk“, Germany)	Late Bithynian–Early Illyrian	263	115	93	11	7	1	12	1	8 Cru 5 Pc 4 O 4 Sc 1 A 1 Pp	Wagner (1897), Schmidt (1928, 1938)
Lapis Limestone (Hungary)	Late Bithynian–Early Pelsonian	23	12	3	2			3		1 M 1 O 1 Sc	Foster and Sebe (2017)
Röt Fm. (“Upper Buntsandstein“, Germany)	Early Bithynian	59	38	3	2		1	1		14 Cru	Wagner (1897), Schmidt (1928, 1938)
Viganvár Limestone (Hungary)	Late Aegean–Early Bithynian	20	10	5	2			1		1 M 1 Sc	Foster and Sebe (2017)
Csopak Marl	Spathian	19	15	3	1			?		? O	Broglio Loriga et al. (1990),

(Hungary)											Budai (2008)
Virgin Fm. (USA)	Spathian	46	30	6	5		1	2	1	1 M	McGowan et al. (2009), Hautmann et al. (2013), Hofmann et al. (2013b), Zatoń et al. (2013b)
Szinpetri Limestone Fm. (USA)	Late Spathian	11	6	2				1		1 M 1 O	Foster et al. (2015)
San Lucano Mb. (Werfen Fm., Italy)	Late Spathian	12	7	4				1			Neri and Posenato (1985), Broglio Loriga et al. (1990), Foster et al. (2017)
Cencenighe Mb. (Werfen Fm, Italy)	Middle Spathian	34	25	6				1		? M 1 O 1 Sc	Neri and Posenato (1985), Broglio Loriga et al. (1990), Hofmann et al. (2015), Foster et al. (2017)
Szin Marl Fm. (Hungary)	Early–Middle Spathian	18	10	4	1			1		1 M ? O 1 Sc	Foster et al. (2015)
Val Badia Mb. (Werfen Fm., Italy)	Early Spathian	23	15	5	1			1		? M 1 O	Broglio Loriga et al. (1990), Hofmann et al. (2015), Foster et al. (2017)
Lower Shale Unit (Thaynes Gr., USA)	Late Smithian–Early Spathian	14	5		3		2	1		2 Cru 1 O	Brayard et al. (2017)
Sinbad Fm. (USA)	Smithian	48	18	27	2		?		?	1 A ? Sc ? O ? Pc	Batten and Stokes (1986), Nützel and Schulbert (2005), Brayard et al. (2011), Hofmann et al. (2014), Villier et al. (2018)
Hidegkút Fm. (Hungary)	Smithian	16	15	1							Bittner (1901), Broglio Loriga et al. (1990)
Campil Mb. (Werfen Fm., Italy)	Smithian	26	21	3	1						Broglio Loriga et al. (1990), Hofmann et al. (2015), Foster et al. (2017)
Zhitkov Fm. (Russia)	Dienerian–Smithian	22	11	8	1			1		? M ? O	Shigeta et al. (2009)

										1 Sc	
Gastropod Oolite (Werfen Fm., Italy)	Late Dienerian–Early Smithian	16	11	4	1					? M	Broglio Loriga et al. (1990), Hofmann et al. (2015), Foster et al. (2017)
Seis Mb. (Werfen Fm., Italy)	Dienerian	24	18	4	1				?	? M ? O 1 Sc	Broglio Loriga et al. (1990), Hofmann et al. (2015), Foster et al. (2017)
Dinwoody Fm. (USA)	Griesbachian–Dienerian	19	15	2	2						Hofmann et al. (2013a)
Köveskál Fm., Arács Fm., Alcsútdoboz Fm. (Balaton Highland, Hungary)	Griesbachian–Dienerian	20	12	7	1						Broglio Loriga et al. (1990)
Lazurnaya Bay Fm. (Russia)	Griesbachian	26	12	6	8						Shigeta et al. (2009)
Bódvaszilas Sandstone Fm. (Hungary)	Middle Griesbachian–Smithian	14	12		1					1 M	Foster et al. (2015)
Luolou Fm. (China)	Middle Griesbachian	30	20	5	3			?	?	? M ? Pc	Hautmann et al. (2015)
Andraz Horizon (Werfen Fm., Italy)	Middle Griesbachian	3	3								Foster et al. (2017)
Mazzin Mb. (Werfen Fm., Italy)	Early–Middle Griesbachian	17	12	3	1					? M 1 Pc	Broglio Loriga et al. (1986, 1990), Hofmann et al. (2015), Foster et al. (2017)
Tesero Oolite (Werfen Fm., Italy)	Late Changhsingian–Early Griesbachian	15	5	3	5			?	1	? M 1 Pc	Broglio Loriga et al. (1986, 1990), Foster et al. (2017)

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Supplementary Material

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